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PUBBLICATI

IN OCCASIONE DEL 50° ANNIVERSARIO

DELLA MORTE

DI FILIPPO BARKER WEBB

EDITA DA

UGOLINO MARTELLI

Professore nella R. Università di Pisa

Webbia Jubilee Issue 1905-2025

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Journal of Plant Taxonomy and Geography (*Webbia*) is a peer-reviewed journal on Plant Taxonomy, Nomenclature, Phylogeny, Phytogeography and Palaeobotany of the Vascular Plants.
The journal aims to allow research in botanical topics such as taxonomy, systematics, nomenclature, molecular phylogeny, conservation, biogeography, and history of botany, and botanical collections.
It was founded in **1905** in Florence by **Ugolino Martelli** (1860-1934), a botanist well known for his studies of and contributions to the systematics of the tropical genus *Pandanus* and on the Flora of Sardinia.
In the 19th century Florence represented one of the most important European centres in Plant Taxonomy and Phytogeography with several notable Italian botanists worth mentioning such as Filippo Parlatore, Teodoro Caruel, Eugenio Baroni, Stefano Sommier, Odoardo Beccari and Ugolino Martelli himself. In 1842 **Filippo Parlatore** (1817-1877) founded in Florence the *Herbarium Centrale Italicum (FI)*, which soon became one of the most important herbaria in the world. Most of the specimens described and/or cited in *Webbia* are still kept in it.
In 1905, and as a consequence of this multitude of activities in Plant Systematics and Phytogeography, Ugolino Martelli established the journal *Webbia-Raccolta di Scritti Botanici*, firstly published annually in a single issue, and later twice a year. Webbia also began to be a place of publication of contributions from Tropical Botany, especially after the Royal Colonial Herbarium founded in 1904 in Rome was moved to Florence in 1914, currently named Tropical Herbarium Study Center (Centro Studi Erbario Tropicale - Herbarium FT) belonging to the Department of Biology of the University of Florence.
Webbia had been created in honor of **Philip Barker Webb** (1793-1845), a close friend of Filippo Parlatore, who before passing away entrusted his personal herbarium and a library rich of old botanical books and publications to the then Botanical Museum in Florence.

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Webbia: 120 years of history between difficulties and milestones

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PROLOGUE

This issue is dedicated to the 120th anniversary of *Webbia*'s founding. It is a fitting tribute to a journal that has been and continues to be a point of reference in the history of Plant Taxonomy and Geography in Italy and abroad. The contributions presented here reflect the journal's international vision, focused on enhancing plant biodiversity in increasingly threatened parts of the World. Thanks go to all the authors present here who responded to my appeal, and for whom I am deeply grateful.

*****

In 1905, the first issue of a new journal on the Italian botanical scene was published. The journal was called *Webbia*, a Latinization of the surname of a great British botanist and benefactor: Philip Barker Webb (1793-1843). The initiative behind this journal was primarily due to a pupil of the Italian botanist Odoardo Beccari (1843-1920) (Fig. 1): Ugolino Martelli (1860-1934) (Fig. 2), who with a *Beccarian impetus* (Lenzi Grillini 1988) and on his 'private' initiative began publishing a new botanical journal on the occasion of the 50th anniversary of P.B. Webb's death. Martelli's initiative was not at all supported by the academic and botanical world of the time (Martelli 1904, 1905a; Lenzi Grillini 1988; Francisco-Ortega et al. 2022). It aroused bitterness between Martelli and the Italian Botanical Society based in Florence, which he recognized as being ungrateful towards the memory of P.B. Webb, who, before his death, had donated to Florence his large and precious collections, a rich botanical library and a financial bequest that could support the preservation of his testimony and legacy for many years.

The first period

In spite of the initial controversies, from 1905 to 1921-1923, *Webbia* was published as a-periodic journal on the private initiative of U. Martelli[1]: from

[1] For a complete biography of U. Martelli see the obituary published on the occasion of his death in 1934 (Negri 1935).

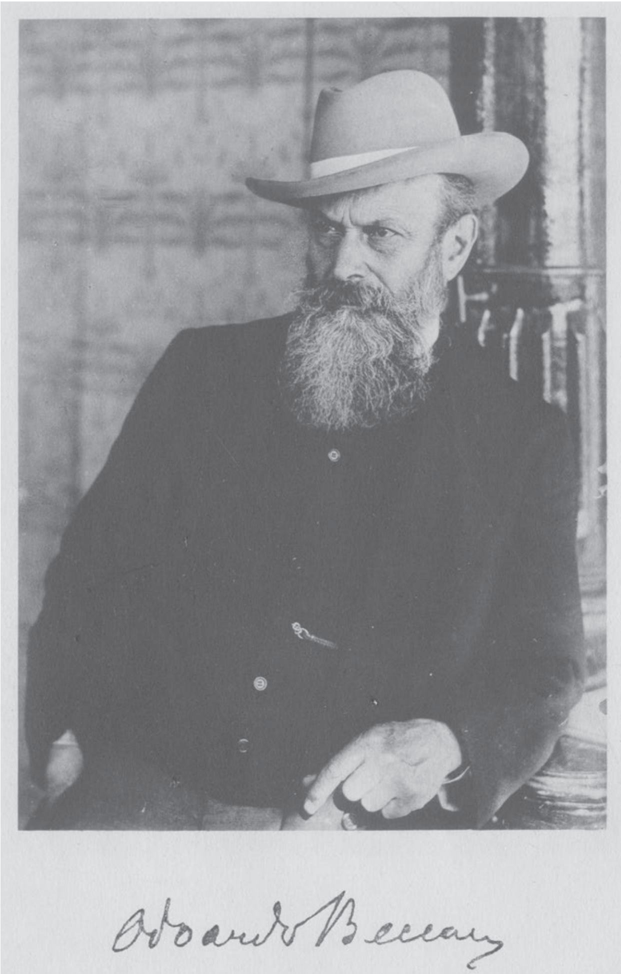

Figure 1. Odoardo Beccari (1843-1920; photo from *Webbia* 5. 1921).

number 1 (1905) to 5 (1921-1923). Despite financial risks assumed by its founder and during this early period, *Webbia* saw the publication of several landmark contributions, such as those of O. Beccari (Beccari 1905a, 1905b, 1905c, 1905d, 1905e, 1907, 1910a, 1910b, 1910c, 1910d, 1910e, 1910f, 1921, 1923), and U. Martelli (1905a, 1905b, 1905c, 1907, 1910a, 1910b, 1910c, 1913, 1914, 1921a, 1921b), as well as those of younger eminent tropical botanists of the period, among them also Chiovenda (1921, 1923), all showing a clear interest verging towards tropical botany [2].

[2] The two papers of E. Chiovenda (1921, 1923) on the origin of *Cocos nucifera* L. published in *Webbia* are part in a broader debate on the origin of the coconut palm, taking place between the end of the 19th and the beginning of the 20th century (see Cook 1901, 1910). O. Beccari himself joined in this debate by enunciating his original theory on the origin and dispersal of *Cocos nucifera* L. (Beccari 1917). 108 years after this publication, O. Beccari's ideas have been recently reviewed, tested in the field and confirmed (Harries et al. 2020; Griffith et al. 2025).

Figure 2. A. Ugolino Martelli (1860-1934); **B.** Front cover of the first issue of *Webbia* (1905). (From Francisco-Ortega et al. 2022).

The number of contributions from O. Beccari and U. Martelli document the influence of both scholars in this early period, both due to their mutual personal and scientific esteem and the devotion of U. Martelli to his master, O. Beccari. The works of O. Beccari and U. Martelli still represent milestones in the study of the Arecaceae and Pandanaceae families. Nevertheless in the first issues between 1905 and 1923, it is possible to find other important contributions on systematics, for example an account of the European Umbelliferae (Calestani 1905), a paper with a review of the history of botany at the time of Linnaeus (Baroni 1905), and a contribution on the Italian Bryophyta (Bottini 1905, 1907, 1913, 1914). Furthermore, U. Martelli's courageous editorial initiative brought O. Beccari back to pro-minence with his last works after his brief stint with the journal *Malesia* (Beccari 1902), which he had founded and financed on his own between 1877 and 1890.[3]

After having started the first issue of *Webbia* with the *Testamento di Filippo Barker Vebb* [The will of

[3] From 1880 O. Beccari retired into a private life, away from the academic world, which he always considered hostile and incompatible with his personal ideas and scientific research. This was the period in which he showed his disappointment with the Botanical Museum and Botanical Garden at 'La Specola' in Florence (Beccari 1881), and during which he began writing his final and most comprehensive work: *Nelle Foreste del Borneo* (Beccari 1902), later translated into English by E. Giglioli and revised and edited by F.H.H. Guillemard (1904) as *Wanderings in the great forests of Borneo*. These works reveal Beccari as a complete, mature, and interdisciplinary naturalist, characteristics not found in many of his contemporaries, who were devoted to academic and often international politics. Complete biographies with list of publications of O. Beccari are available in works by Pichi Sermolli and van Steenis (1979-1983) and Pichi Sermolli (1994).

Philip Barker Webb] and a personal correspondence of the latter, U. Martelli concluded his editorial task with the fifth issue, which he dedicated to O. Beccari on the occasion of his death in 1920 at the age of 77 after an intense life full of vicissitudes that made O. Beccari a sort of myth of tropical plant systematics. Lately, the last of O. Beccari's posthumous work (Beccari† and Pichi Sermolli 1956) was published under the supervision and curatorship of R.E.G. Pichi Sermolli (1912-2005) (Fig. 3, 4), 33 years after the publication of the fifth issue of *Webbia*. It is clear how the first five issues of *Webbia* were inspired by the deep friendship and esteem of U. Martelli towards his teacher and mentor O. Beccari.

However, U. Martelli, in the preface to the second issue published in December 1907, did not hesitate to express his hope that *Webbia* in due time would become a regular periodical journal, appealing to those friends and colleagues who had appreciated the publication since its first issue in 1905. This was a legitimate and desirable wish, but it was not entirely realized since *Webbia* by then had not yet achieved the status of a truly regular periodical.[4]

However, financial unsustainability, combined with a hostile environment in the academic field led U. Martelli to cease publication of the journal in 1923, beginning a 27-year period of silence.

Figure 3. Rodolfo Emilio Giuseppe Pichi Sermolli (1912-2005) at Kew in 1947. (Courtesy of R.E.G. Pichi Sermolli family).

The transition period between the two world wars and post-war reconstruction until the 21st century

From the interwar period until the end of the Second World War, the official and most important journal of the Italian Botanical Society was the *Giornale Botanico Italiano*, later *Nuovo Giornale Botanico Italiano*, currently *Plant Biosystems*. It served as the primary point of reference for Italian botanical publishing, although with a number of other journals (Lenzi Grillini 1988). As described by Lenzi Grillini, the war period was a test of self-denial on the part of prominent Italian scientists such as, for example, Alberto Chiarugi, who had to fight even under semi-clandestine conditions in order to keep the Italian Botanical Society alive. The desire for redemption after Italy's tragic war-experience led to

[4] In the preface to the second issue published in December 1907, U. Martelli expressed hope for a truly regular periodical status for *Webbia*:

Prefazione
"Quando nell'Aprile dell'anno 1905, per onorare la memoria di un illustre botanico inglese, benemerito della nostra scienza in Italia, io pubblicai una piccola raccolta di scritti botanici sotto il titolo Webbia*, non ebbi in animo di iniziare una pubblicazione periodica; ma la buona accoglienza fatta a quel volume mi ha dato coraggio ad invitare nuovamente alcuni chiarissimi amici e colleghi a favorirmi dei lavori per comporne un secondo portante lo stesso titolo. Con ciò non intendo fare promesse per il futuro, né dare un carattere di regolare periodicità alla '*Webbia*'; se però, come spero, l'esito del presente volume non sarà inferiore a quello del primo, mi propongo di farne seguire altri più o meno sollecitamente. Rivolgo intanto agli amici collaboratori i miei ringraziamenti".*

[Preface
"When, in April 1905, to honor the memory of an illustrious English botanist who had contributed greatly to our science in Italy, I published a small collection of botanical writings under the title 'Webbia,' I had no intention of starting a periodical. However, the warm reception to that volume encouraged me to once again invite some very distinguished friends and colleagues to contribute their work to a second volume bearing the same title. With this, I do not intend to make any promises for the future, nor to establish a regular periodicity for 'Webbia'; however, if, as I hope, the outcome of this volume is not inferior to that of the first, I intend to publish others more or less promptly. In the meantime, I extend my thanks to my collaborators."].

Da Firenze, Dicembre 1907

Prof. Ugolino Martelli

Figure 4. Rodolfo Emilio Giuseppe Pichi Sermolli in Addis Ababa (6th October 1966), receiving from the hands of Emperor Hailé Selassié an Ethiopian imperial award for his studies and investigations on the Flora and Vegetation of Ethiopia, most of them published in *Webbia* (Photo from an Ethiopian newspaper via Ib Friis).

the birth and rebirth of new publishing tools. In this context, thanks to the initiative of the phytogeographer Giovanni Negri (1877-1960), *Webbia* saw its rebirth as the official organ of the Botanical Institute of the University of Florence, at the same time as the founding of the *Centro per lo Studio della Flora e Vegetazione Italiana* [Center for the Study of Italian Flora and Vegetation] as part of the *Centro Nazionale delle Ricerche* [National Research Center], founded years earlier in 1923.

Webbia saw its new debut with a monograph by R.E.G. Pichi Sermolli entitled *Flora e vegetazione delle serpentine e delle altre ofioliti dell'alta valle del Tevere (Toscana)*, [Flora and vegetation of the serpentines and other ophiolites of the Upper Tiber Valley (Tuscany)]. It is interesting to point out that Giovanni Negri was advised by R.E.G. Pichi Sermolli, as heir of the *Beccarian* tradition, to resume the publication of *Webbia* in an institutional form and based in Florence. Later, it is worth mentioning, under the direction of Alberto Chiarugi (1901-1960), that the volume 11 of *Webbia* was published in 1956 on the occasion of the centenary of the death of Philip Barker Webb (Chiarugi 1956a) in which *Beccarian* ideas of global botany are celebrated after many years with the publication of 19 monographs on tropical flora, but also with contributions on Italian flora, including the monumental study on the flora and vegetation of the island of Marettimo (Egadi Islands) by Francini and Messeri (1956).

Between 1953 and 1978, Webbia published a series of 34 monographs on the flora of the Horn of Africa, with the common heading *Adumbratio Florae Aethiopicae*.[5] This ambitious project was based on the valuable botanical collections of the *Erbario Coloniale Italiano* [Italian Colonial Herbarium], later the *Erbario Tropicale di Firenze* [Tropical Herbarium of Florence (FT)], currently the *Centro Studi Erbario Tropicale dell'Università*

[5] The complete bibliography of *Adumbratio Florae Aethiopicae* can be found in the bibliography section in Baldini (2010). The translation into English of the Latin title *Adumbratio Florae Aethiopicae* could be *Description of Ethiopian Flora*, remembering that *Aethiopia* (Ethiopia) is taken in a broad sense as explained by Chiarugi in his introduction to the project.

di Firenze (FT) [Tropical Herbarium Study Center of the University of Florence (FT)]. The aim and objectives of the *Adumbratio Florae Aethiopicae* were well described in the introduction by Alberto Chiarugi (Chiarugi 1953), introducing the historical and geographical contexts of the project.[6] One of the milestones in this period is represented by the publication in *Webbia* of *Una carta geobotanica dell'Africa Orientale (Eritrea, Etiopia, Somalia)* [A geobotanical map of Eastern Africa (Eritrea, Ethiopia, Somalia)] by Pichi Sermolli (1957) followed 8 years later by the *Map of the extent of the floristic exploration in Africa South of the Sahara* by Léonard (1965)[7]. Furthermore, in 1963 *Webbia* hosted the *Proceedings of the Fifth Symposium of A.E.T.F.A.T. (Association pour l'Étude Taxonomique de la Flore de l'Afrique Tropicale)* organized by R.E.G. Pichi Sermolli, a publication later commented on by Hepper (1963)[8].

Lately, under the direction of Guido Moggi (1960-1963; 1976-1999)[9], followed a period lasting 27 years, during which the journal opened the doors also to 'heretical' authors like the Italian Leon Croizat (1894-1982)[10,11]. During these years, *Webbia* continued hosting international monographs and proceedings of international symposia (Chiarugi 1956b; Heywood and Pichi Sermolli 1961[12]; Pichi Sermolli 1965[13]; Moggi 1979, 1992) (Fig. 5). Since 1948 until at least the nineteen-nineties, *Webbia* maintained its strong tropical legacy, although it gradually became more focused on studies of the flora and vegetation of Italy and the Mediterranean area becoming a landmark for many Italian and foreign researchers. This is the transition time between the dominant role of *Webbia* in the scenario of the Plant Taxonomy and Geography in Italy and up to the impact of the new century, the 21st, in which publishing underwent a change towards increasing competition, both in Italy and abroad.

However, contributions of international significance for both Italy and the world continued to be published in *Webbia*, rediscovering the journal's tropical vocation in the issue 60(1). 2005[14], a monograph revision of about 400 pages on the pteridological collections made in Brazil by Giuseppe Raddi (1770-1829), thanks to R.E.G. Pichi Sermolli, who died a few days after its publication in April 2005, while he was working on his planned last work on the ferns of Ethiopia and Eritrea (Pichi Sermolli and Bizzarri 2005)[15].

In this period of time, Italy also witnessed a proliferation of other botanical journals, often reflecting the provincial sentiment of having a journal for each academic institution, rather than national Italian ones. However, before the advent of the strong international editorial competition, and partly due to new printing and distribution technologies, *Webbia* continued to be a point of reference for the Plant Taxonomy and Geography of Italy and other countries.

With the advent of important and significant new researches, particularly with molecular techniques, plant taxonomic publishing underwent rapid change, and not all journals, including *Webbia*, immediately grasped the momentum of this transformation. Added to this global phenomenon was the transformation of botany from an autonomous discipline to a more fragmented one.

The fragmentation of Plant Taxonomy and Geography increasingly pushed young botanists to consider it

[6] Chiarugi (1953), in his introduction to the *Adumbratio Florae Aethiopicae*, not only illustrates the aim of the project, but also the criteria of the study and the choice of the overall territory, which includes Ethiopia, Eritrea, Somalia and the Soqotra Archipelago, a choice based on phytogeographical, historical and cultural evidence.

[7] These contributions should be added to other subsequent ones that have encouraged the study of the flora and vegetation of Africa (White 1976, 1983, 1993a, b).

[8] R.E.G. Pichi Sermolli was member of the A.E.T.F.A.T.-UNESCO Vegetation Map Committee and contributed with material from the Horn of Africa to the A.E.T.F.A.T.-UNESCO Vegetation Map of Africa published by White (1983).

[9] Under the careful direction of Guido Moggi, *Webbia* rapidly expanded its influence in Italy and abroad, attracting authors of international value.

[10] In the 1960s, thanks to the foresight of its director, Guido Moggi, *Webbia* hosted the contributions of Leon Croizat, the father of *panbiogeography* or the subsequent *cladistic biogeography*, in the wake of the teachings developed by the Italian zoologist Daniele Rosa (1857-1944), supporter of the *theory of hologenesis*, then pursued further by the German entomologist Willi Hennig (see Hennig 1950; Croizat 1952, 1958a, 1958b, 1958c, 1962; Llorente et al. 2000; Morrone 2006, 2021; Williams and Ebach 2008; Mahlfeld and Parenti 2023). L. Croizat, not having received much recognition in the scientific community of the time, thanked *Webbia* for the opportunity to freely disseminate his ideas, confirming *Webbia's* inclusive stance compared to other journals of the time. It is worth mentioning that L. Croizat dedicated a paper on *panbiogeography* published in *Webbia* to his friend R.E.G. Pichi Sermolli (Croizat 1973).

[11] At the end of the third chapter on the infrageneric classification of the genus *Euphorbia* focused on the South African and Malagasy areas, L. Croizat points out the role of *Webbia* in the diffusion of his monographic works thanking the attentiveness of the Director Guido Moggi (Croizat 1972) as follows:

"*As a parting statement, I wish to express heartfelt thanks to Prof. Dr. Guido Moggi for his thoroughly open-minded – contrary to inured editorial usage, so particular in Anglo-Saxon and socialist countries – acceptance of this long series of articles. Should their readers agree that they have derived some increment of knowledge from what they impart, they ought to feel no less grateful to the Editor than to the author, if ever. It has virtually become impossible to find today takers for literature which enters the field of general ideas and method beyond the stale limits of a standard 'technical paper'.*

[12] A further example of cultural inclusiveness beyond territorial and ideological borders was the hosting of scientists from both opposing political blocs during the Cold War at the second Flora Europea symposium.

[13] The photo in Fig. 4 was kindly provided by Paola Bizzarri.

[14] The issue 60(1) was published on occasion of the 100 years since the foundation of *Webbia*.

[15] A fond memory of R.E.G. Pichi Sermolli was written by his dear colleague and friend R.K. Brummitt (Brummitt 2007).

Figure 5. Participants in the Fifth Meeting of the *Association pour l'étude taxonomique que de la Flore d'Afrique tropical (A.E.T.F.A.T.)* held in Genoa and Florence on the 9th-14th September 1963. Photo taken at the Botanical Garden of Florence (Courtesy of Paola Bizzarri). Legend: (1) A.Y.M. Leeuwenberg; (2) G. Moggi; (3) Ake-Assi; (4) A. Getahun; (5) A. Aubreville; (6) J. Leonard; (7) R.E.G. Pichi Sermolli; (8) A. Fernandes; (9) H. Wild; (10) J. Aymonin; (11) E. Milne Readhead; (12) O. Hedberg; (13) F. White; (14) R. Corti; (15) A.W. Exell; (16) F.N. Hepper; (17) H. Heine; (18) B. Peterson; (19) J.B. Gillett; (20) G. Cufodontis; (21) A.M. Raynal; (22) M.P. Bizzarri; (23) M. Kerauden; (23) E. Francini Corti; (25) R. Fernandes; (26) I. Hedberg.

old-fashioned and *boring*, trapped into an ever-increasing scientific reductionism (Crisci 2008; Muller 2018; Crisci et al. 2020; Baldini et al. 2021) that influenced botanical publishing including *Webbia*.

The world changed and the competition became increasingly hard even for Webbia

Thus, the scientific editorial scenario changed in the last 20 years, producing an epochal novelty in which the ways of publishing and spreading of scientific knowledge were literally shocked, especially by the latest technological innovations in the editorial field. The introduction of metric evaluations such as the *devilish* number called *impact factor* not only subverting the idea of global science but also contaminating the idea of *Academia* as a repository of knowledge and experience, and above all the methods according to which university recruitment could be carried out, based on statistical-algorithmic assessments, and forgetting often the quality of scientific experience and production of new knowledge (Krell 2000; Woodland 2007; Garwood 2013[16]; Stephan et al. 2017; Müller 2018).

Due to strategic local editorial mistakes in the first years of XXI century, *Webbia* suffered during the new era due to academic provincialism and competition from *predatory journals*, unethical publications that prioritize profit over scholarly integrity and often lacking proper reviews. The fate of *Webbia* went into the hands of a few people, often the Editor in Chief alone, and even in conjunction with difficulties at financial and management level. These were hard times that saw *Webbia* abandoned by most of the Italian audience due also to the logic (or illogic?) of the university recruitment based on citation metrics, impact factor, and other scholarly dynamics,

[16] As reported in Garwood (2013: 19) "(...) *the journal IF* [impact factor] *was developed to help librarians make subscription decisions. (...) Researchers are now judged by "where" they publish and not by "what" they publish"; "The IF obsession is warping our scientific judgement, damaging careers, and wasting time and valuable works*".

often questionable with regard to the progress of science. Since the beginning of my role as Editor in Chief in 2008 until 2013, *Webbia* tried to survive with great difficulty until it landed at a British Publisher: Taylor & Francis. This went on until, finally, in 2020 *Webbia* came *back home*, beginning a new improving opportunity and collaboration with the Florence University Press (FUP) (Fig. 6). In collaboration with FUP, it has been possible to publish more proceedings of symposia (see Baldini 2015, 2017, 2018), and supplement monographs (Delprete 2022; Friis et al. 2022; Wong 2023[17]).

In the time span of 120 years seven botanists have managed the direction of *Webbia* (Fig. 7, 8):

Ugolino Martelli: Vol. 1 (1905) - Vol. 5 (1923).
Giovanni Negri: Vol. 6 (1948).
Alberto Chiarugi: Vol. 7 (1950) - Vol. 14 (1960).
Eleonora Francini Corti: Vol. 18 (1963) - Vol. 29 (1975).
Guido Moggi: Vol. 15 (1960) - Vol. 17 (1963), and Vol. 30 (1976) - Vol. 53 (1999).
Mauro Raffaelli: Vol. 54 (1999) - Vol. 62 (2007).
Riccardo Maria Baldini: Vol. 63 (2008) - Vol. 80 (2025).

In the recent volumes, rediscovery and reevaluation of plant taxonomy, as well as new aspects of the history of botany, have been recorded, especially in studies in overseas countries, confirming the importance of the *traditional and historical* approaches as an essential basis for achieving more advanced and refined results. In this regard, as the current Editor in Chief, I must express my thanks to those who have believed in *Webbia* and supported its cause, especially in recent years (see also Baldini 2025).

Some data about Webbia since its foundation: the proof that Plant Taxonomy and Geography have always existed and still are alive and well

The contribution of *Webbia* to the knowledge of plant taxonomy can be evaluated by the number of botanical names published from its foundation in 1905 to the current year, 2025, after 120 years of activities. If we consider as a whole, new species, subspecies, varieties, forms and new supraspecific categories such as new families, genera, tribes, sections etc., including also new combinations, and new names, their number, according to the International Plant Names Index (IPNI 2025) database, reached 1982 names until 2021 and, adding to this the names from the latest years until 2025, a total amounting to 2212 names. This is an appreciable result in an increasingly competitive international publishing scenario permitted also by the current synergy between *Webbia* and the *Centro Studi Erbario Tropicale (FT herbarium)*.

[17] Sin Yeng Wong's work on the genera of Borneo is also a tribute and reminder of O. Beccari's immense contribution to the study of the Malaysian Flora.

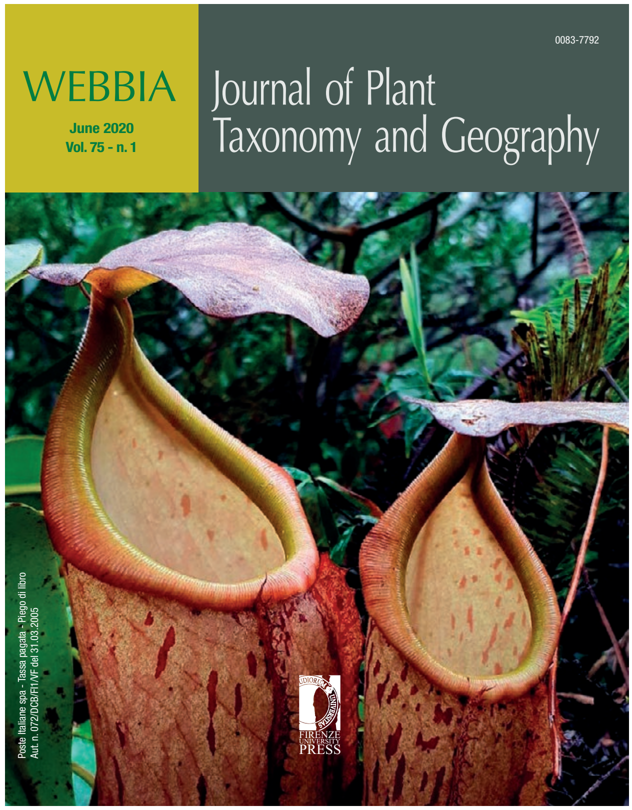

Figure 6. Front cover of the first issue published by Firenze University Press in 2020.

This positive trend can only be improved thanks to the future understanding of the new plant taxonomists, which I hope will continue to grow. It seems paradoxical in an era where we hear ever increasing demand for more and more *biodiversity*, as if that concept, but perhaps without that name, had never existed in the minds of taxonomists and biologists, or among non-scientists as well.[18]

The rediscovery and development of classical taxonomic and geographical methods, varying from more intense field research to deeper herbarium study, better

[18] There's no doubt that in recent years, the word 'biodiversity' has been used in the mainstream as if no one had addressed this issue in the past. However, consulting journals like *Webbia* and similar publications we understand how many Italian and foreign researchers have addressed *biodiversity*, perhaps without using the specific term, and have contributed to the knowledge of the fundamentals for environmental issues that today are often addressed by neophytes unaware of past literature.

Figure 7. Left top: Giovanni Negri (1877-1960); right top: Alberto Chiarugi (1901-1960); left bottom: Eleonora Francini Corti (1904-1984); right bottom: Guido Moggi (1927-) (photos from Moggi 2006).

mapping techniques based on much more material, and finally to integration with new phylogenetic and phylogeographic methodologies, will lead to the reaffirmation of Plant Taxonomy and Geography in its broadest senses, rediscovering its true operational meaning and usefulness for future generations.

I hope that young taxonomists will rediscover and re-evaluate what patience in research and the use of historical-comparative approach can achieve in combination with new methods, eschewing the easy solutions and the frenzy of publishing as well as relying on the predation of many journals that are nothing more than sneaky baits.

120 years of taxonomic, phytogeographical and floristic history represent a long time and should make us reflect on how many people have employed their intellectual forces to achieve a deeper knowledge of plants and ultimately a better world. Because our masters are often forgotten or ignored, journals like *Webbia*, covering more than a century, may hopefully help new generations of botanists to rediscover the link between historical and future meaning of Plant Taxonomy and Geography, often at risk of being left without the historical legacy. It is my hope that a look at the history of *Webbia* may help the coming generations to rediscover the central role of Plant Taxonomy and Geography in the study of biodiversity and the distribution of plants.[19]

Figure 8. Left hand: Mauro Raffaelli (1944-), photo from Moggi (2006); right hand: Riccardo Maria Baldini (1958-).

In this, *Webbia* and other botanical journals with a long history may have a surge of pride for the future: this is, at least, my hope.

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[19] These methodological aspects are well summarized in White (1971, 1993a) and emphasized by Thompson et al. (2018).

REFERENCES[20]

Baldini RM. 2010. The contribution of the Florentine collections to the knowledge of the Flora of Ethiopia and Eritrea. Acta Universitatis Upsaliensis, Symbolae Botanicae Upsalienses. 35(2): 161-171.

Baldini RM. (Ed.). 2015. Proceedings of Symposium "100 years of the Tropical Herbarium in Florence (1914-2014) held in Florence on the 3rd of October 2014. Webbia. 70(1): 155-198.

Baldini RM. (Ed.). 2017. Proceedings of Symposium "Past, Present and Future in Tropical Botany: Taxonomy, Data Archiving and Genomics" held in Florence on 21st October 2016. Webbia. 72(1): 1-51.

Baldini RM. (Ed.). 2018. Proceedings of Symposium "Bicentenary of Giuseppe Raddi's Journey to Brazil" held in Florence on the 5-6 October 2017. Webbia. 73(1): 107-174.

Baldini RM, Pignotti L. 2020. Correction to Candollea 75: Unraveling the taxonomic identity of *Cocos nucifera* f. *palmyrensis* (Arecaceae: Cocoseae). Candollea. 75(2): 321.

Baldini RM, Cota-Sánchez JH, Aedo C. 2021. Is the demise of plant taxonomy in sight? Maybe yes, maybe no… . Webbia. 76(1): 3-10.

Baldini RM. 2025. Editorial. Webbia. 80(1): 3.

Baroni E. 1905. Sopra l'Erbario di Linneo; manoscritto inedito di F. Parlatore. Webbia. 1: 75-83.

Beccari O. 1881. Sull'abbandono del Museo e del Giardino Botanico della Specola a Firenze. Protesta dei cultori della Botanica in Firenze colle adesioni e le osservazioni dei Botanici italiani e stranieri. Tipografia B. Sborgi, Firenze. Pp.1-72.

Beccari O. 1902. Nelle foreste di Borneo. Viaggi e ricerche di un naturalista. Tipografia Salvatore Landi, Firenze.

Beccari O. 1905a. Le Palme del genere "*Trachycarpus*". Webbia. 1: 41-73.

Beccari O. 1905b. Note anatomiche sul frutto dei *Trachycarpus*. Webbia 1: 68-72.

Beccari O. 1905c. Notizie sul "*Nannorhops ritchieana*" H.Wendl. Webbia. 1: 72-73.

Beccari O. 1905d. Palme nuove papuane. Webbia. 1: 281-313.

[20] The most significant works from the first issues of *Webbia* here cited show the reaction to U. Martelli's initiative: only the attentiveness of colleagues and trusted friends of him allowed the beginning of *Webbia*, certainly not the general botanical *academia* of the time around U. Martelli. Martelli's merit was to allow the publication of major contributions that have shaped the history of taxonomy in Italy and abroad. Martelli's initial sense of frustration with the academic environment (see Martelli 1905a) was comparable only to that experienced by his master O. Beccari in the most part of his life.

Beccari O. 1905e. Le Palme delle Isole Filippine. Webbia. 1: 315-359.

Beccari O. 1907. Le Palme americane della Tribù delle Corypheae. Webbia. 2: 1-339.

Beccari O. 1910a. Studio monografico del genere *Raphia*. Webbia. 3: 37-130.

Beccari O. 1910b. Palme Australasiatiche nuove o poco note. Webbia. 3: 131-165.

Beccari O. 1910c. Descrizione di una nuova specie di *Trachycarpus*. Webbia. 3: 187-190.

Beccari O. 1910d. Palme dell'Indo-China. Webbia. 3: 191-245.

Beccari O. 1910e. Contributo alla conoscenza delle Lepidocaryeae affricane. Webbia. 3: 247-294.

Beccari O. 1910f. La *Copernicia cerifera* in Riviera ed una nuova specie di *Livistona*. Webbia. 3: 295-305.

Beccari O. 1913. Contributo alla conoscenza delle Palme. Webbia. 4(1): 143-240.

Beccari O. 1914a. Manipolo di Palme nuove polinesiane conservate nell'erbario di Kew. Webbia. 4(2): 253-291.

Beccari O. 1914b. Studio sui "*Borassus*". Descrizione di un genere nuovo asiatico di "Borasseae". Webbia. 4(2): 293-385.

Beccari O. 1917. Origin and dispersal of *Cocos nucifera*. Philippine Journal of Science. C12: 27-43.

Beccari O. 1921. Recensione delle Palme del Vecchio Mondo appartenenti alla Tribù delle Corypheae. Webbia. 5(1): 6-146. Tav. I-XIII.

Beccari O. 1923. Note botaniche e botanico industriali bornensi. Webbia. 5(2): 451-584.

Beccari O (†), Pichi Sermolli REG. 1956. *Subfamiliae Arecoidearum Palmae Gerontogeae, Tribuum et Generum conspectus*. Webbia. 11: 1-188.

Bottini A. 1905. Frammenti di Briologia Italiana. Webbia. 1: 17-24.

Bottini A. 1907. Sulla Briologia delle Isole Italiane. Webbia. 2: 346-402.

Bottini A. 1913. Sulla briologia di Corfù. Webbia. 4(1): 241-248.

Bottini A. 1914. Sfagni d'Italia. Supplemento I. Webbia. 4(2): 387-397.

Brummitt RK. 2007. R.E.G. Pichi Sermolli (1912-2005). Taxon. 56(4): 1304-1307.

Calestani V. 1905. Contributo alla sistematica delle Ombrellifere d'Europa. Webbia. 1: 89-280.

Chiarugi A. 1953. *Adumbratio Florae Aethiopicae* 1 – *Introductio*. Webbia. 9: 1-8.

Chiarugi A. 1956a. Nel primo centenario della morte di Philip Barker Webb, 1854-1954. Webbia. 11: ix-xviii.

Chiarugi A. (Ed.). 1956b. Proceedings of the Second Meeting of the "Association pour l'etude taxonomique

que de la Flore d'Afrique tropicale (A.E.T.F.A.T.)", held in Oxford on the 30th of September-2nd October 1953. Webbia. 11: 387-403; 405-412; 413-423; 424-450; 452-466; 467-469; 471-487; 489-496; 497-517; 519-523; 525-540; 541-585.

Chiovenda E. 1921. La Culla del Cocco. Contributo alla ricerca della patria originaria della Palma del Cocco. Webbia. 5(1): 199-294.

Chiovenda E. 1923. La Culla del Cocco. Contributo alla ricerca della patria originaria della Palma del Cocco. Webbia. 5(2): 359-449.

Cook OF. 1901. The origin and distribution of the Cocoa Palm. Contributions from the United States National Herbarium. 7(2): 257-293.

Cook OF. 1910. History of the Coconut Palm in America. Contributions from the United States National Herbarium. 14(2): 271-342.

Crisci JV. 2008. La barbarie del "especialismo" en un tiempo de extinciones. Anales de la Academia Nacional Agronomía Veterinaria, Buenos Aires. 62: 97-107.

Crisci JV, Katinas L, Apocada MJ, Hoch PC. 2020. The end of botany. Trends in Plant Sciences. 25(12): 1173-1176.

Croizat L. 1952. Manual of Phytogeography. An Account of Plant-Dispersal throughout the World. Uitgeverij Dr. W. Junk, The Hague.

Croizat L. 1958a. Panbiogeography. Vol. I. The New World. Caracas (Venezuela, S.A.). Published by the Author.

Croizat L. 1958b. Panbiogeography. Vol. IIa. The Old World. Caracas (Venezuela, S.A.). Published by the Author.

Croizat L. 1958c. Panbiogeography. Vol. IIb. The Old World (continuation). Caracas (Venezuela, S.A.). Published by the Author.

Croizat L. 1962. Space, Time, Form: The Biological Synthesis. Caracas (Venezuela, S.A.). Published by the Author.

Croizat L. 1972. An introduction to the subgeneric classification of "Euphorbia" L., with stress on the South African and Malagasy species. III. Webbia. 27(1): 1-221.

Croizat L. 1973. La "Panbiogeografia" in breve. Webbia. 28(1): 189-226.

Delprete PG. 2022. Monograph of the tribe Sipaneeae (Rubiaceae, Ixoroideae). A Neotropical group with its center of diversity on the Guiana Shield. Webbia. 77(1) Suppl.: 1-284.

Francini E, Messeri A. 1956. L'Isola di Marettimo nell'Arcipelago delle Egadi e la sua vegetazione. Webbia. 11: 607-846.

Friis I, Demissew S, Weber O, van Breugel P. 2022. Plants and vegetation of NW Ethiopia. A new look at Rodolfo E.G. Pichi Sermolli's results from the "Missione di Studio al Lago Tana" 1937. Firenze: Firenze University Press. Pp. 7-350.

Krell FT. 2000. Impact factors aren't relevant to taxonomy. Nature. 405: 507-508.

Francisco-Ortega J, Baldini RM, Manning JC, Gandhi KN. 2022. Honoring Philip Barker Webb: the three intriguing stories of *Webbia* as a genus name. Webbia. 77(1): 3-21.

Garwood J. 2013. Time to Change How Research is Assessed. Lab Times. 5: 18-23.

Griffith MP, Stauffer F, MacLaughlin K, Gerrish J, Baldini RM. 2025. *Cocos nucifera* var. *palmyrensis*, a Unique Native Coconut from Palmyra Atoll. Palms. 69(2): 83-102.

Hennig W. 1950. Grundzüge einer Theorie der phylogenetischen Systematik. Deutsche Zentralverlag, Berlin.

Harries HD, Pignotti L, Baldini RM. 2020. Unraveling the taxonomic identity of *Cocos nucifera* f. *palmyrensis* (Arecaceae: Cocoseae). Candollea. 75(1): 25-30.

Hepper FN. 1963. The Flora of Tropical Africa. Nature. 200: 530-531 [published on 9th November 1963].

Heywood VH, Pichi Sermolli REG. (Eds.). 1961. Proceedings of the Second Flora Europaea Symposium, held in Genoa on the 21st-28th May 1961. Webbia. 18: 1-562.

IPNI. 2025. International Plant Names Index. Published on the Internet http://www.ipni.org, The Royal Botanic Gardens, Kew, Harvard University Herbaria & Libraries and Australian National Herbarium [Retrieved 17 July 2025].

Lenzi Grillini C. 1988. Cento anni di editoria botanica in Italia. In: Pedrotti F. (Ed.), 100 anni di ricerche botaniche in Italia (1888-1988). Società Botanica Italiana, Firenze. Pp. 1069-1109.

Léonard J. 1965. Map of the extent of floristic exploration in Africa South of the Sahara. Webbia. 19(2): 907-914.

Llorente J, Morrone JJ, Bueno A, Pérez-Fernandez R, Viloria Á, Espinosa D. 2000. Historia del desarrollo y la recepción de las ideas panbiogeográphicas de Léon Croizat. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales. 24(93): 549-577.

Mahlfeld K, Parenti LR. 2023. Croizat's form-making, RNA networks, and biogeography. History and Philosophy of the Life Sciences. 45(1): 42-53.

Martelli U. 1904. Per la ricorrenza del cinquantesino anniversario della morte di Filippo Barker Webb. Bullettino della Società Botanica Italiana. 1904: 231-232.

Martelli U. 1905a. Prefazione. Webbia. 1: v-xi.
Martelli U. 1905b. Presentazione di un libro dal titolo Webbia. Bullettino della Società Botanica Italiana. 1905: 165.
Martelli U. 1905c. *Pandanus*. Nuove Specie Descritte. Webbia. 1: 361-371.
Martelli U. 1907. *Pandanus*. Nuove specie. Manipolo II. Webbia. 2: 423-438.
Martelli U. 1910a. Le *Freycinetia* delle isole filippine. Webbia. 3: 5-35.
Martelli U. 1910b. Nuove specie di *Freycinetia*. Webbia. 3: 167-186.
Martelli U. 1910c. Enumerazione delle Pandanaceae. Webbia. 3: 307-327.
Martelli U. 1913. Enumerazione delle Pandanaceae. Webbia. 4(1): 5-105.
Martelli U. 1914. Le specie e varietà nuove di "*Pandanus*" menzionate nella Enumerazione delle Pandanaceae. Webbia. 4(2): 399-435. Tab. I-XLIII.
Martelli U. 1921a. Odoardo Beccari. Webbia. 5(1): 295-343.
Martelli U. 1921b. Opere botaniche del Dott. O. Beccari. Webbia. 5(1): 344-353.
Moggi G. (Ed.). 1979. Proceedings of the O.P.T.I.M.A. Meeting, held in Florence on the 23rd-29th May 1977. Webbia. 34(1): 1-551.
Moggi G. (Ed.). 1992. Proceedings of the Meeting "150 HCI, Botanical Collections and Scientific Research" held in Florence on 16th-18th September 1992. Webbia. 48: 1-849.
Moggi G. 2006. Webbia 1905-2005. 100 anni di ricerche tassonomiche e fitogeografiche in Italia. Webbia. 61(1): 193-206.
Morrone JJ. 2006. La vita tra lo spazio e il tempo. Il retaggio di Croizat e la nuova biogeografia. (a cura di Mario Zunino). Medical Books, Palermo.
Morrone JJ. 2021. Croizat's dangerous ideas: practices, prejudices, and politics in contemporary biogeography. History and Phylosophy of the Life Sciences. 43(2): 1-45.
Müller JZ. 2018. The Tyranny of Metrics. Princeton University Press, Princeton & Oxford.
Nergi G. 1935. Ugolino Martelli 1860-1934. Nuovo Giornale Botanico Italiano, n.s. 42: 1-16.
Negri G. 1948. Premessa. Webbia. 6: vii-viii.
Pichi Sermolli REG. 1948. Flora e Vegetazione delle serpentine e delle altre ofioliti dell'Alta Valle del Tevere (Toscana). Webbia. 6: 3-378.
Pichi Sermolli REG. 1957. Una carta geobotanica dell'Africa Orientale (Eritrea, Etiopia, Somalia). Webbia. 13(1): 15-132. [21 figures & 1 geographic map].
Pichi Sermolli REG. (Ed.). 1965. Proceedings of the Fifth Meeting of the "Association pour l'etude taxonomique que de la Flore d'Afrique tropicale (A.E.T.F.A.T.)" held in Genoa and Florence on the 9th-14th September 1963. Webbia. 19(2): 491-914.
Pichi Sermolli REG., 1994. Odoardo Beccari: vita, esplorazioni, raccolte e scritti del grande naturalista fiorentino. 70. Fratelli Alinari, Firenze.
Pichi Sermolli REG, Bizzarri P. 2005. A revision of Raddi's pteridological collection from Brazil (1817-1818). Webbia. 60(1): i-viii, 1-394.
Pichi Sermolli REG, van Steenis CGGJ. 1979-1983. Dedication. Flora Malesiana. ser. I, vol. 9: 6-44.
Raimondo FM. (Ed.). 1984. Proceedings of the 4th O.P.T.I.M.A. Meeting held in Palermo on the 6th-14th June 1983. Webbia. 38: 1-845.
Stephan P, Veugelers R, Wang J. 2017. Blinkered by bibliometrics. Nature. 544: 411-412.
Thompson SA et al. 2018. Taxonomy based on science is necessary for global conservation. PLOS Biology. 16(3): e2005075. https://doi.org/10.1371/journal.pbio.2005075.
White F. 1971. The taxonomic and ecological basis of chorology. Mitteilungen der Botanischen Staatssammlung München. 10: 91-112.
White F. 1976. The vegetation map of Africa: the history of a completed project. Boissiera. 24: 659-666.
White F. 1983. The vegetation of Africa. A descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation of Africa. UNESCO.
White F. 1993a. The AEFTAT chorological classification of Africa: history, methods and applications. Bulletin du Jardin botanique national de Belgique. 62: 225-281.
White F. 1993b. Refuge theory, ice-age aridity and the history of tropical biotas: an essay in plant geography. Fragmenta Floristica et Geobotanica Supplementum. 2(2): 385-409.
Williams DM, Ebach MC. 2008. Foundations of Systematics and Biogeography. Springler Science +Business Media, LLC. e-ISBN: 978-0-387-72730-1.
Wong SY. 2023. Flora of Borneo: the vascular plant genera. Webbia. 78(1). Suppl.: 5-309.
Woodland DW. 2007. Are botanists becoming the dinosaurs of biology in the 21st century? South African Journal of Botany. 73(3): 343-346.

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The species of Burseraceae in Ethiopia – their distribution patterns, association with major vegetation types, species richness, and extinction risks

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Abstract. The Burseraceae in Ethiopia comprises six species of *Boswellia* and 42 of *Commiphora*, producing frankincense or myrrh. This work aims to study the distribution and ecology of all 48 species, although some *Commiphora*-species are poorly documented. *Boswellia* species form two distinct geographic groups: one northwestern and one southeastern. Most *Commiphora* species are confined to the southern and eastern lowlands, with a few also occurring in river valleys in highlands. Distributions are analysed against vegetation types and climate models. Ranges vary from widespread in climatically suitable areas to highly localized. *Commiphora* species are linked to *Acacia-Commiphora* bushland on limestone and sand (mostly calcareous), though specific ecological preferences are still unclear. Species richness on degree squares correlates with collection intensity, indicating gaps in knowledge beyond well-sampled areas. Assessed IUCN categories of extinction risks range from Least concern to Critically endangered.

Keywords: *Acacia-Commiphora* woodland and bushland, *Combretum-Terminalia* woodlands, conservation, modelled distributions, observed distributions.

INTRODUCTION

The commonly known aromatic resins used as incense, frankincense and myrrh, are obtained from the dried sap of shrubs or small, deciduous trees of the genera *Boswellia* and *Commiphora* in the plant family Burseraceae. The genus is known to occur in nearly all tropical African countries, but almost always restricted to lowland areas with one or several prominent dry seasons. The species are all adapted to a dry season by being deciduous. In the countries that harbour most *Boswellia* and *Commiphora* species, frankincense and myrrh provide a unique resource that supplements the limited incomes among the local rural population. However, many species of *Com-*

miphora are affected by the increasing size and necessities of the human population in their natural habitats, causing destruction of the habitats, and the as yet not well understood effects of climate change. In Ethiopia, two species have been assessed as critically endangered, seven species as near threatened, six species as vulnerable, sixteen species as least concern, while the status of fifteen species is still unsettled on the Red List of the IUCN, where the different levels of extinction risks are presented (https://www.iucnredlist.org/).

The use of incense, almost certainly from species of Burseraceae, has been documented by the presence of incense burners found in archaeological sites in Ethiopia and Yemen from the pre-Aksumite period, and incense has been an important commercial good since the Antiquity. The ancient Egyptians imported incense from the areas around the southern part of the Red Sea and the Gulf of Aden (Bulakh and Fiaccadori 2007).

In Ethiopia, incense is still much in use, being burnt with charcoal to produce perfumed smoke, either in censers for church use or on open burners of clay for private use. Recently, the production of incense in Ethiopia has been estimated at over 30,000 tons annually, though the largest part is consumed internally and only (in 1995–2000) between 800 and 1800 tons were exported (Volker-Saad 2007). Incense from species of Burseraceae has been important in the rites of the Ethiopian Orthodox Church since the beginning of the 4th Century; currently, the use of incense is compulsory during every service except at the rites of penance (Fritsch 2007). The resins from species of *Boswellia* and *Commiphora* seem also to play an increasing role in the pharmaceutical industry (Eltigani et al. 2025).

There are no longer difficulties with the taxonomy and distribution of *Boswellia* in Ethiopia, but there are still problems with the taxonomy and distribution patterns of *Commiphora*. In the Flora of Ethiopia, Vollesen (1989) provided a detailed account of six species of *Boswellia* and 52 species of *Commiphora*. In his account for the Flora of Tropical East Africa (Burseraceae), Gillett (1991) provided an account of four species of *Boswellia* and ca. 44 species of *Commiphora* recorded from Kenya, mainly in the part of the country closest to Ethiopia and Somalia. In the Flora of Somalia, Thulin (1999) provided the taxonomy of three species of *Boswellia* and 52 species of *Commiphora* of which seventeen species did not occur in Ethiopia. Despite the presence of these good accounts, taxonomic problems persisted, and it is never easy for users to identify or collect good material of the species because leaves, flowers, and fruits are needed for certain identification, and they are rarely available on the same shrub or tree at the same time.

It is worth mentioning that the theme of this work follows in the tradition of the journal Webbia, providing both taxonomic and phytogeographical works on the Horn of Africa. Already the first detailed vegetation map of Ethiopia (Pichi Sermolli 1957) documented the importance of species of Burseraceae in the Ethiopian lowland vegetation in a long and detailed paper in Webbia. This has been further emphasised on the two recent vegetation maps of Ethiopia (Friis et al. 2010, 2022), published as monographs for which precursory studies have appeared in Webbia. Another Italian botanist, Emilio Chiovenda, published most of his important studies on the flora of the Horn of Africa, mainly Somalia, in other outlets than Webbia, but here we should mention his main work on the Burseraceae, the Flora Somala 2 (Chiovenda 1932), which together with his other publications on the family is frequently cited here.

As part of the preparation of a new Field Guide to species that produce frankincense and myrrh in Ethiopia (Demissew and Friis in preparation), the present authors have collected data of all *Boswellia* and *Commiphora* species from Ethiopia, concluding on a moderately modified taxonomy in relation to that of Vollesen (1989), with the number of species of *Commiphora* in Ethiopia reduced to 42.

Although the genus *Boswellia* occurs in both the western and the eastern lowlands of Ethiopia, the genus *Commiphora* is almost entirely restricted to the south-eastern and adjacent lowlands with very variable patterns of distribution, ranging from widespread species in many habitats to local endemics probably found only on a narrow range of geological formations. A few species penetrate into the highlands along the deep river valleys of the Tacazze, Abay, Gibe, Didessa, and Omo. This work is intended to summaries what we currently know and can conclude about the distributions of the species of Burseraceae in Ethiopia, which may help attempts at their conservation.

MATERIALS AND METHODS; PRESENTATION OF DATA

Extensive data gathered by the authors from the Burseraceae collections in the herbaria at C, ETH, FT, and K, as well as from our own field observations, all based on carefully identified specimens. Ca. 910 identified collections were listed and their sites of collection georeferenced, using all available sources to identify the coordinates of the localities of the collections. We used the GIS software ArcGis 9 / ArcMap 9.3 to map the collections and produce the maps with the distribution of the collections superimposed on a map of vegetation types of Ethiopia. The layers and the legend of these vegetation types (Fig. 1A & 1B) have been adapted from Friis et al. (2022, Fig. 4-1) and are used for all the distribution maps with direct observations in this work.

The modelling in this work of suitability of habitats was based on the sample of the ca. 910 identified and georeferenced collections and was made with MaxEnt, vers. 3.4.4 (Phillips 2017). The results produced with the MaxEnt-analyses were further treated with DivaGis 7.5.0 (Hijmans et al. 2012) to adjust the classes of climatic suitability to five intervals: from not suitable (0) to highly suitable (1), represented in this paper with suitability 0–0.2 (dark green), 0.2–0.4 (light green), 0.4–0.6 (yellow), 0.6–0.8 (orange), and 0.8–1.0 (dark red). The files used for climatic parameters were derived from the internet database in WorldClim (2020–2025), representing the years 1970-2000, and with a spatial resolution of 30 seconds, which is comparable to a pixel size of ca. 1 km^2. The parameters are: 1 = Annual Mean Temperature; 2 = Mean Diurnal Range (Mean of monthly max temp - min temp); 3 = Isothermality (parameters 2 / parameters 7 ×100); 4 = Temperature Seasonality (standard deviation ×100); 5 = Max Temperature of Warmest Month; 6 = Min Temperature of Coldest Month; 7 = Temperature Annual Range (parameter 5 - parameter 6); 8 = Mean Temperature of Wettest Quarter; 9 = Mean Temperature of Driest Quarter; 10 = Mean Temperature of Warmest Quarter; 11 = Mean Temperature of Coldest Quarter; 12 = Annual Precipitation; 13 = Precipitation of Wettest Month; 14 = Precipitation of Driest Month; 15 = Precipitation Seasonality (Coefficient of Variation); 16 = Precipitation of Wettest Quarter; 17 = Precipitation of Driest Quarter; 18 = Precipitation of Warmest Quarter; 19 = Precipitation of Coldest Quarter.

Species with only one record are mapped but cannot be modelled with MaxEnt. The reliability of the modelled distributions of species with more than one record relies strongly on the number of observed occurrence points (locations of collections with documented occurrence) and the relevant environmental parameters that are involved in the analyses (Merow et al. 2013; Phillips 2017; Lissovsky and Dudov 2021). The minimum number of observed occurrence points varies with their geographical distribution and the reliability of the environmental parameters. As suggested by Paulo van Breugel (pers. com.) in connection with discussions of how to draw conclusions of this study, results of modelling may not be expected to reliably model species with below approximately 12–13 observed occurrence points. However, for endemic Ethiopian species the number of observed occurrence points must of necessity be lower, and we have for example used a limit of 5–6 of observed occurrence points. Nevertheless, for the sake of completion, we have run models for all species with two or more observed occurrence points, but we have not offered special comments on the reliability of the result based on modelled omission rates in relation to the expected values in cases with fewer than 12–13 observed occurrence points (Ethiopian endemics excepted). For species with sufficient number of occurrence points, we suggest if the model is performing as intended or not, based on the curve showing the modelled omission rate, in other cases we simply present the model without commenting on how reliably it may function.

We are fully aware that MaxEnt, as pointed out by Lissovsky and Dudov (2021), does not provide a "magic wand" that in all cases will provide a correct modelled range map. Nevertheless, we hope that our study presents useful steps forward both with regard to observations, modelling, understanding of relation to vegetation types and distribution patterns of the Burseraceae in Ethiopia.

For both the distribution maps on vegetation types and for the maps showing modelled suitability, the outlines of the lakes of Ethiopia have been superimposed with blue colour and a black border-line. Likewise, the borders of the floristic regions of the Flora of Ethiopia and Eritrea have been superimposed both on the maps showing observed distributions (with thin black border-lines), and on the maps showing modelled potential distributions (with bold black border-lines). A map with the border lines of these floristic regions is published opposite the title page of the first published volume of the Flora of Ethiopia [and Eritrea] and republished in all subsequent volumes. The floristic regions are: AF (Afar region, below and to the east of the 1000 m contour to the Eritrean border in the east and to the Harerge border in the south); TU (abbreviation of Tigray Uplands, area within the former outline of the Tigray region above and to the west of the 1000 m contour); GD (the former Gonder region); GJ (the former Gojam region); WU (abbreviation of Welo Uplands, area within the former Welo region above and to the west of the 1000 m contour); SU (abbreviation of Shewa Uplands, area within the former Welo region above and to the west of the 1000 m contour); AR (the former Arsi region); WG (the former Welega region); IL (the former Illubabor region); KF (the former Kefa region); GG (the former Gamo Gofa region); SD (the former Sidamo region); HA (the former Harerge region).

DivaGis 7.5.0 was also used as a tool to analyse the distributions of the data on one-degree squares. This included indication of number of observed positive presence locations on one-degree squares of all records used in this paper, estimation of richness of Burseraceae species on one-degree squares with direct observation, and rearranged richness with Jackknife cross-validation technique (Hijmans et al. 2012: 35–36) to reduce bias in parameter estimates, as well as estimation of diversity of Burseraceae on one-degree squares measured with the Shanon-Wiener Index (Hijmans et al. 2012: 38), applying both richness (number of species) and evenness (how evenly individuals are distributed among species). We have also tried to perform the analyses with quarter-degree squares but found that the very uneven distribution of the occurrence points observed made it even more difficult to find a pattern of richness that would make sense with the topography and climate.

Although geological suitability would also have represented important environmental parameters to use for this study, perhaps as important as the climatic parameters we were able to use, we were only able to find traditional geological maps (Tefera et al. 1996; Last 2009), but no high-resolution digital data sets suitable for incorporating geological formations in our analyses. Instead, we have summarized the information about substrates and vegetation types from available sources, including Flora of Ethiopia, Flora of Tropical East Africa, and Flora of Somalia and attempted to make a verbal summary in our conclusions.

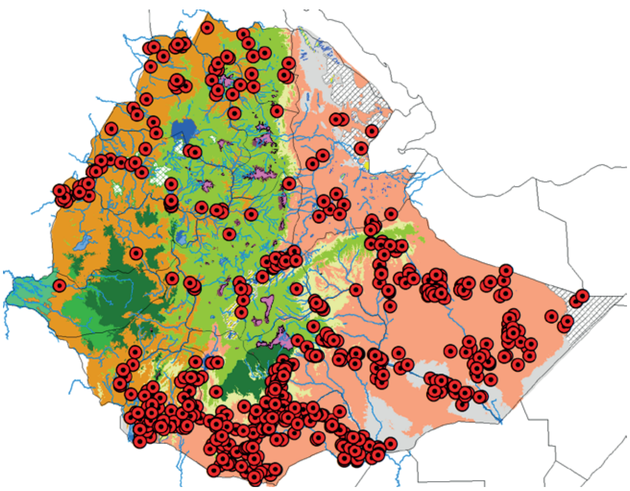


Figure 1A. Distribution of all ca. 910 records of Ethiopian Burseraceae studied for this work and superimposed on the vegetation types defined in Friis et al. (2022). The same classification of vegetation types is used on the left-hand maps in the Figs. 3–50. For legend to the vegetation types, see Fig. 1B.

Both because of the small number of occurrence points for many species and the non-random distribution of occurrence points in geographical space, often densely clustered in well-collected areas but perhaps erroneously absent in poorly collected areas, the results of our modelling will for many species require data correction from future collections.

The assessed extinction risk is cited where available and is available for species endemic to Ethiopia. We have not attempted to assess EOO (Extent of Occurrence) and AOO (Area of Occupancy) with GeoCAT (https://geocat.iucnredlist.org/) for species that occur outside Ethiopia due to our lack of information about their entire distribution, and therefore not indicate more about general threat of these species. A summary is given in our conclusions and in Table 4.

The taxonomy and sequence of species in this work follows the manuscript of our drafted Field Guide (Demissew and Friis in preparation). A number of synonyms have been cited in this work to ensure the option for reliable comparison with the regional floras (Vollesen 1989; Gillett 1991; Thulin 1999; 2020).

GENERAL DISTRIBUTION OF BURSERACEAE IN ETHIOPIA

The distribution of the total number of species of Burseraceae in Ethiopia is mapped on Fig. 1A, based on data from this study. The distribution of the species is modelled on the suitability of climatic parameters as presented in Fig. 2, with the use of DIVA-GIS. It appears from Fig. 1A that most records studied have been found growing in *Acacia-Commiphora* woodland and bushland proper in southern and southeast-

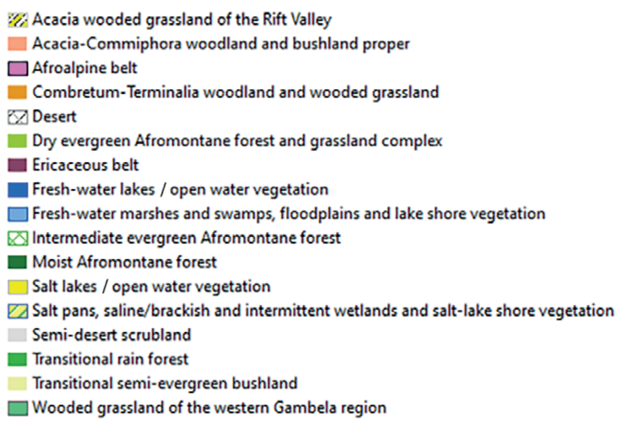


Figure 1B. Legend to vegetation types defined in Friis et al. (2022) and used for all distribution maps in this paper.

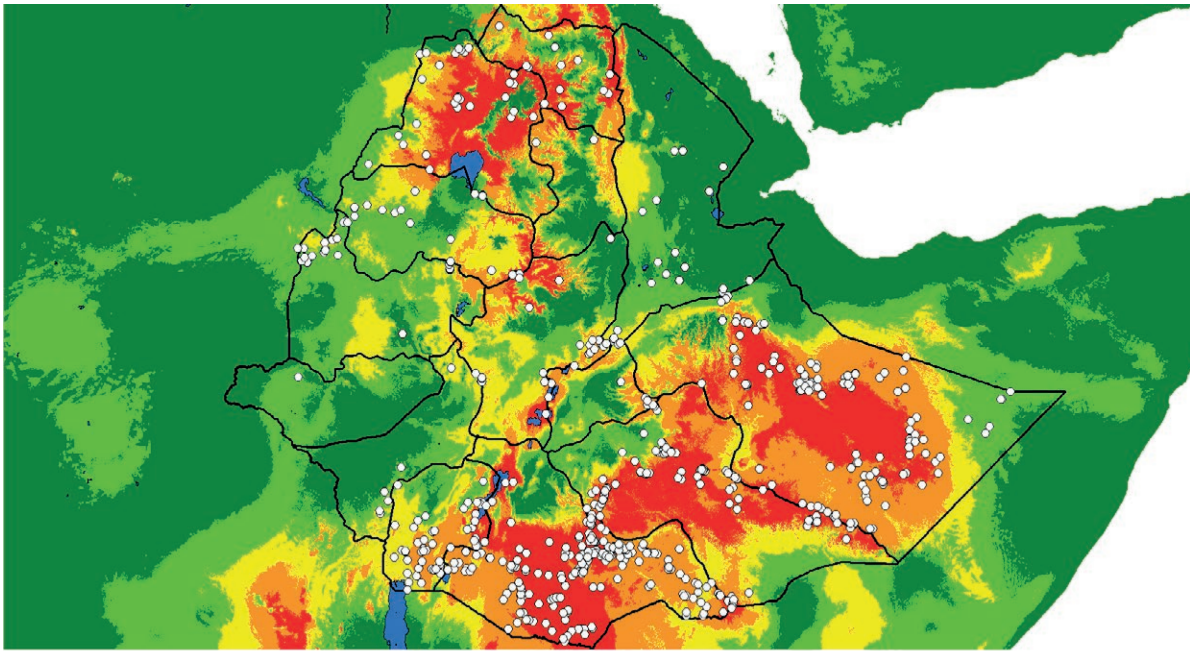


Figure 2. Map showing modelled suitability of potential distribution areas of the species of Burseraceae in Ethiopia, based on climatic parameters. The legend to the colouring is the same as for all maps in this paper showing potential vegetation: Dark green: Suitability 0–0.2. Pale green: Suitability 0.2–0.4. Yellow: Suitability 0.4–0.6. Orange: Suitability 0.6–0.8. Red: Suitability 0.8–1.0.

ern Ethiopia, but many records have also been made in transitional semi-evergreen bushland, which represents the transition zone between lowland and highland vegetation (Friis et al. 2010, 2022). A number of species in these two areas of distribution belong to the genus *Boswellia*, but many more to the genus *Commiphora*. Although most species grow in *Acacia-Commiphora* woodland and bushland proper, some may also grow in *Combretum-Terminalia* woodland and wooded grassland on the western side of the Ethiopian highlands and in the deep river valleys.

The modelled map in Fig. 2 shows that most of our records of Burseraceae occur in areas with the highest category of suitability, dark red, but a number of records have been collected from areas with the two lowest categories of suitability, pale green and dark green, the latter is most often the case with records from AF, the Afar region.

STUDY OF HABITATS AND DISTRIBUTION OF INDIVIDUAL SPECIES

In the following, mapping and modelling of each of the six species of *Boswellia* and the forty-two species *Commiphora* are dealt with as represented by ca. 910 collections we have studied. If possible, the treatment for each species includes, as for the two separate maps showing all species in Fig. 1A and Fig. 1B, figures with a combination of two maps, to the left a map of observed distribution on vegetation types and to the right a map showing a combination of observed records and modelled distribution based on climatic parameters. The number of observed occurrence points are cited in the text for each species. Collections of *Boswellia* and *Commiphora* that could not be identified to species are not included, and data relating to infraspecific taxa, except for the subspecies *C. edulis* subsp. *boiviniana*, are not accounted for here. For all species we have tried to add the general distribution and, according to the latest Red List of IUCN (https://www.iucnredlist.org/), the extinction risk of the species.

B01. ***Boswellia papyrifera*** (Caill.) Hochst., Flora 26: 81. 1843.

Fifty occurrence points studied, which we consider sufficient for reliable modelling. The species is distributed in *Combretum-Terminalia* woodland and wooded grassland on the western side of the Ethiopian highlands as far south as the northern part of WG but the species does also occur in the deep valleys of the rivers running both westwards towards the Abay and eastwards towards the Awash rivers. In the latter, an isolated population is

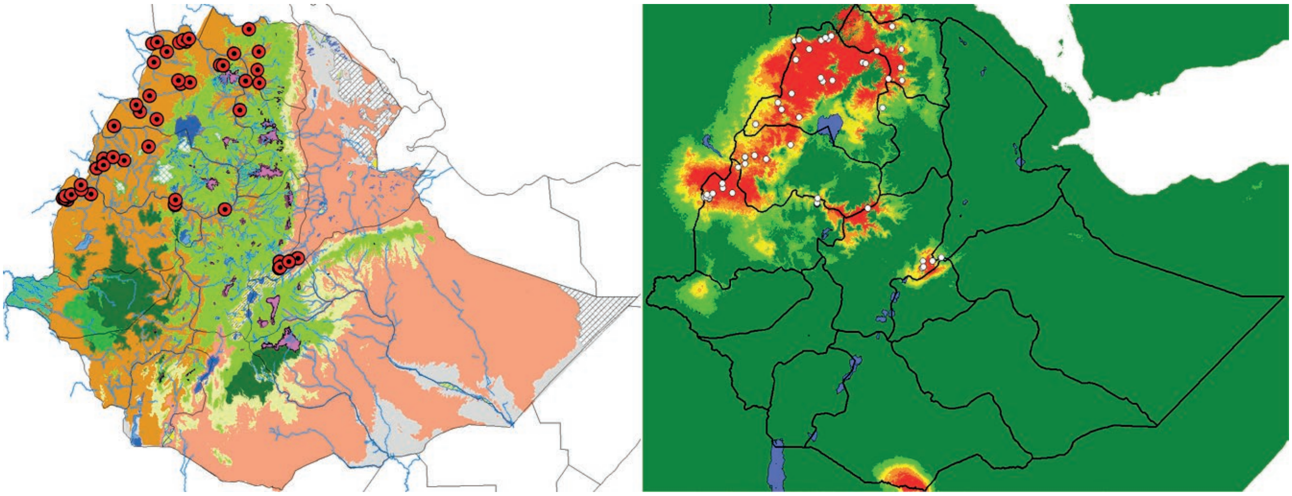


Figure 3. *Boswellia papyrifera* (Caill.) Hochst. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see B01.

found in vegetation recorded as *Acacia-Commiphora* woodland and bushland (Fig. 3).

There is good agreement between the areas of the actual and the modelled distribution, and the modelled omission rates of *B. papyrifera* are close to the expected values, suggesting that the model performs as intended. The highest contribution to the model is provided by Bio19 (precipitation of coldest quarter).

In Ethiopia, the species has been reported to grow in dry *Acacia-Commiphora* woodland and wooded grassland [but this is not the typical habitat], in *Pterocarpus* woodland, a northern subtype of *Combretum-Terminalia* woodland, often as the dominant species on steep rocky slopes, also on lava flows (Vollesen 1989). In Tropical East Africa (Uganda), it has been found growing on stony hillsides in dry wooded grassland (Gillett 1991). Thulin (2020) cites that in Ethiopia this is a characteristic species of the northern half of the vegetation types designated as *Combretum-Terminalia* woodland and wooded grassland, which is confirmed by studies of Friis et al. (2022) and here.

The species is widespread in deciduous woodlands of northern tropical Africa from Nigeria to Sudan (Darbyshire et al. 2015), Eritrea and Ethiopia, reaching southwards to Uganda. The species is of economic importance, and population studies have been made of mature trees and their regeneration (Abiyu et al. 2010).

Thulin (2020) assessed the extinction risk as Vulnerable A2cd + 3cd. Despite the evidence cited by Thulin (2020), *B. papyrifera* is not currently red-listed by IUCN. Previous IUCN information can be found at https://doi.org/10.2305/IUCN.UK.2018-2.RLTS.T34394A128137387.en.

B02. ***Boswellia pirottae*** Chiov., Ann. Bot. (Rome) 9: 53. 1911.

Twenty-nine occurrence points studied, which we consider sufficient for reliable modelling. The species is mainly found below and near the upper limit of *Combretum-Terminalia* woodland and wooded grassland on the western side of the Ethiopian highlands from GD in the north to the northernmost part of WG and KF in the south. The river valleys in the highlands with *B. pirottae* comprise the Abay Valley, running to the west, and an apparently isolated population in the upper part of the Omo Valley, running to the south. There seems to be no population in rivers running to the east (Fig. 4).

There is good agreement between actual and modelled distributions, and the modelled omission rates of *B. pirottae* are close to the expected values, suggesting that the model performs as intended. The highest contribution to the model is provided by Bio19 (precipitation of coldest quarter).

The species has been reported to grow in *Commiphora-Boswellia*, *Combretum* and *Acacia-Lannea* woodland on steep rocky slopes (Vollesen 1989), and more generally in variants of *Combretum-Terminalia* woodland (Thulin 2020; Friis et al 2022). The substrate is according to our own observations usually derived from basaltic rocks, usually where these rocks form steep slopes.

The species is endemic to Ethiopia. The extinction risk of the species is considered Vulnerable C1 by Awas T, Belay B, Demissew S, Nemomissa S, Mekbib E, Atnafu H, Alemu S, Alemu S. 2021. *Boswellia pirottae* (errata version published in 2022). The IUCN Red

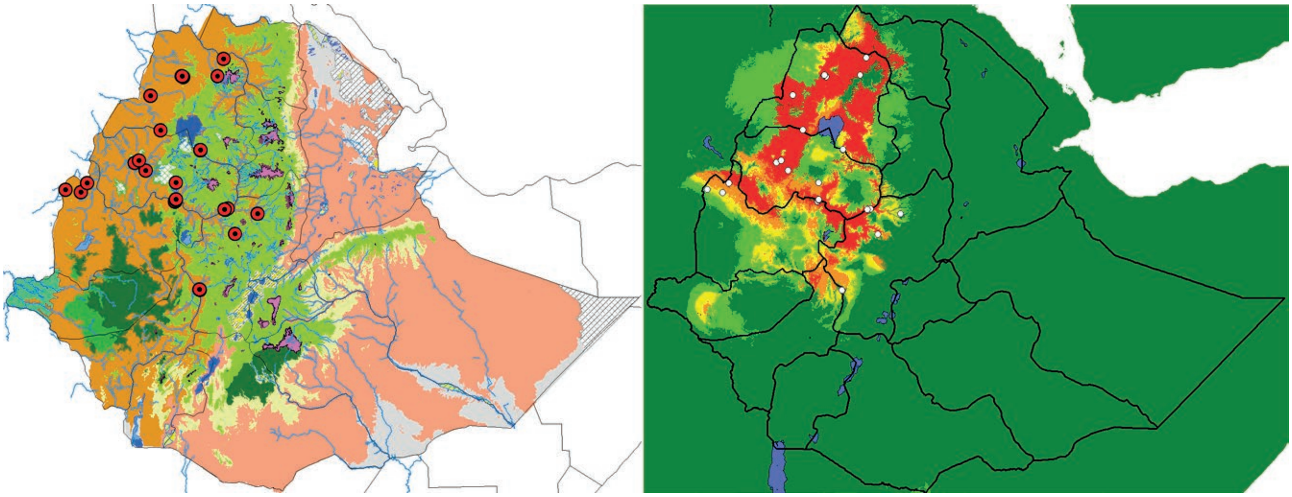


Figure 4. *Boswellia pirottae* Chiov. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see B02.

List of Threatened Species 2021: e.T34394A223071850. https://doi.org/10.2305/IUCN.UK.2021-3.RLTS.T34394A223071850.en. The species is assessed to have a continuing decline of mature individuals and a continuing decline in area, extent and/or quality of habitat. Thulin (2020) suggested the same assessment extinction risk.

B03. ***Boswellia rivae*** Engl., Ann. Bot. (Rome) 7: 16. 1897.

(=) *B. boranensis* Engl., Bot. Jahrb. Syst. 34: 316. 1904.

Twenty occurrence points studied, which we consider sufficient for reliable modelling. The species is restricted to *Acacia-Commiphora* woodland and bushland proper in southern and southeastern Ethiopia, with slight transgression into transitional semi-evergreen bushland, semi-desert scrubland, desert, and saline wetlands (Fig. 5).

There is good agreement between the recorded distribution and area of highest suitability, and the modelled omission rates of *B. rivae* are close to the expected value, suggesting that the model performs as intended. The highest contribution to the model is provided by Bio11 (mean temperature of coldest quarter).

In Ethiopia, it has been reported to grow in *Acacia-Commiphora* wooded grassland and bushland on red sandy soil overlying limestone (Vollesen 1987). In Tropical East Africa (Kenya), it has been found growing in open *Acacia-Commiphora* bushland on limestone hills (Gillett 1991). In Somalia, it has been reported from both the northern, central and southern parts, growing in open *Acacia-Commiphora* bushland, often on hills or rocky ridges, usually on limestone, occasionally on gypsum (Thulin 1999, 2020).

Restricted to Ethiopia, Somalia, northeastern Kenya. The extinction risk of the species is considered Least Concern by Alemu S, Alemu S, Atnafu H, Awas T, Bahdon J, Belay B, Demissew S, Luke WRQ, Mekbib E, Musili P, Nemomissa S. (2021). *Boswellia rivae* (errata version published in 2022). The IUCN Red List of Threatened Species 2021: e.T128044164A223074935. https://doi.org/10.2305/IUCN.UK.2021-3.RLTS.T128044164A223074935.en. Although considered Least Concern, the species is assessed to have a continuing decline in area, extent and/or quality of habitat. Thulin (2020) has suggested the same assessment.

B04. ***Boswellia ogadensis*** Vollesen, Kew Bull. 40: 39. 1985.

Two occurrence points studied. Although this is a species endemic to Ethiopia, two records are not sufficient for reliable modelling, but as far as known, the species is restricted to a part of semi-desert scrubland, desert, and saline wetlands along the lower reach of the Webe Shebele River (Fig. 6).

The species is reported to grow in *Acacia-Commiphora* bushland on rocky limestone slopes (Vollesen 1989), where, according to Thulin (2020), it is restricted to gypseous ground.

Endemic to Ethiopia.

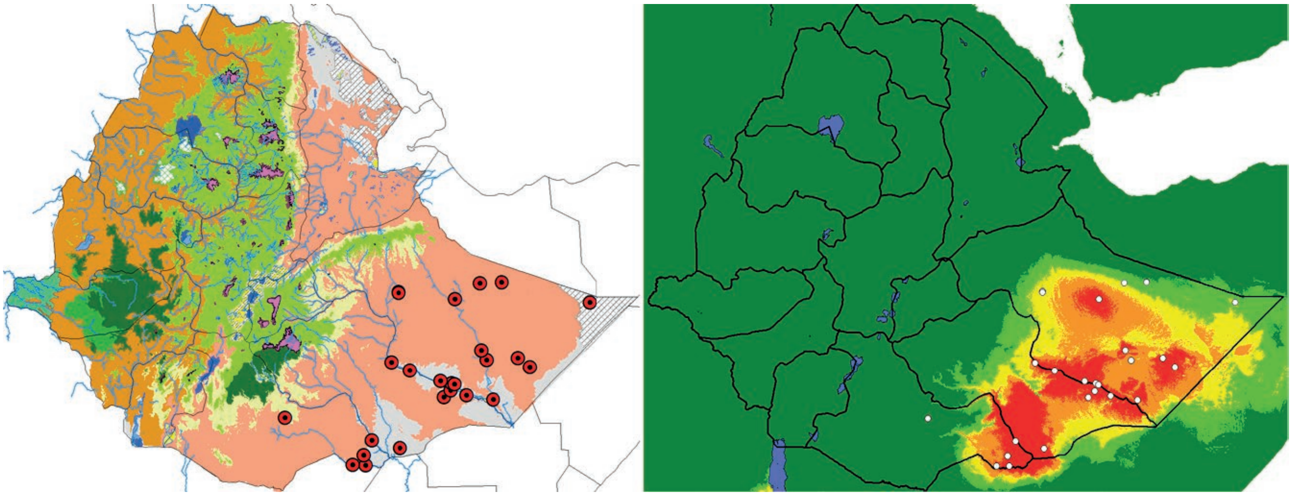


Figure 5. *Boswellia rivae* Engl. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. The westernmost outlying collection in SD was included in the modelling but is not in the predicted area. For text about species, see B03.

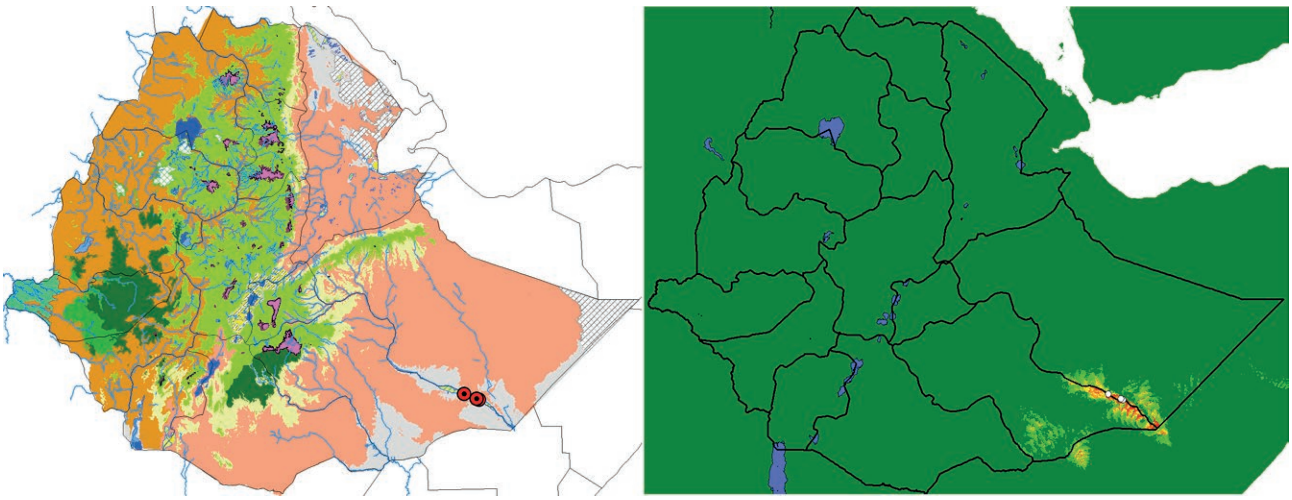


Figure 6. *Boswellia ogadensis* Vollesen in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see B04.

The extinction risk of the species is considered Critically Endangered B1ab(iii) by Alemu S, Alemu S, Atnafu H, Awas T, Belay B, Demissew S, Luke WRQ, Mekbib E, Nemomissa S, Bahdon J. 2021. *Boswellia ogadensis* (errata version published in 2022). The IUCN Red List of Threatened Species 2021: e.T34385A223070932. https://doi.org/10.2305/IUCN.UK.2021-3.RLTS.T34385A223070932.en. The populations are severely fragmented and there is a continuing decline of mature individuals. Thulin (2020) has suggested the same assessment.

B05. ***Boswellia neglecta*** S.Moore, J. Bot. 15: 67. 1877.

Sixty occurrence points studied, which we consider sufficient for reliable modelling. The species is restricted to *Acacia-Commiphora* woodland and bushland proper in southern and southeastern Ethiopia, with slight transgression into semi-desert scrub and transitional semi-evergreen bushland; it has not been recorded from the Afar region (Fig. 7).

There is good agreement between the recorded distribution and area of highest suitability, and the mod-

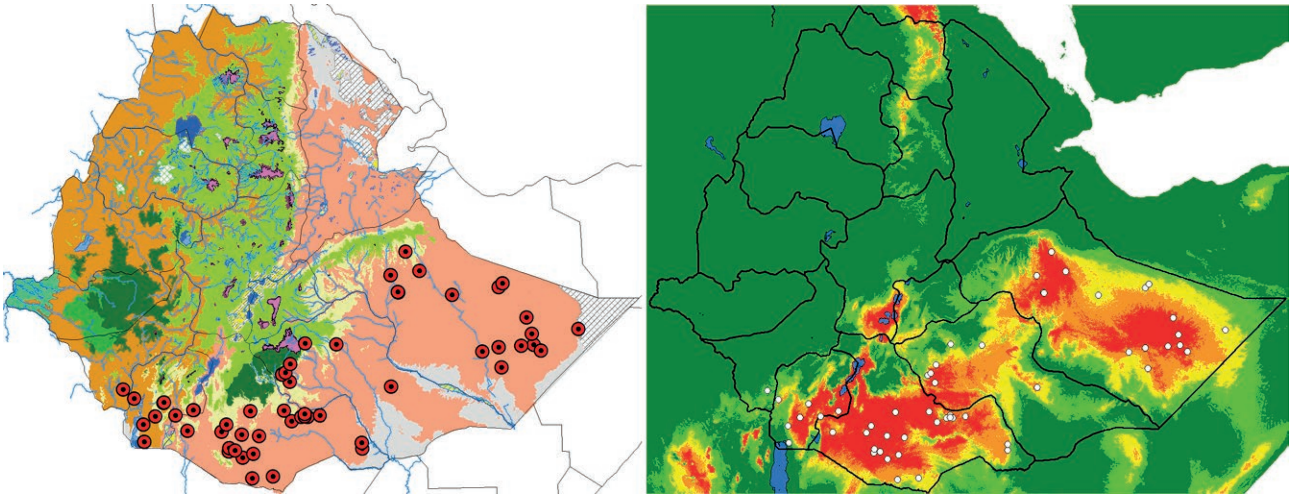


Figure 7. *Boswellia neglecta* S. Moore in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see B05.

elled omission rates of *B. neglecta* are close to the expected value, suggesting that the model performs as intended. The highest contribution to the model is provided by Bio3 (isothermality).

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* woodland, wooded grassland and bushland, *Acacia-Boswellia-Terminalia* woodland or wooded grassland, often on red sandy soil overlying limestone but also on basement rocks (Vollesen 1989). In Tropical East Africa (Uganda, Kenya, Tanzania), it has been found growing in *Acacia-Commiphora* bushland on basement complex or lava and red sandy soil (Gillett 1991).

Thulin (1999) considered *B. neglecta* and *B. microphylla* as one variable species, but kept them distinct in Thulin (2020), according to which it has been known from both the northern, central and southern parts, growing in *Acacia-Commiphora* bushland, usually on red sandy soil overlying limestone but also on basement rocks and on lava.

In Ethiopia, Somalia, northeastern Uganda, northern and eastern Kenya, northeastern Tanzania. Not red-listed by IUCN. Thulin (2020) has preliminarily suggested an assessment of the extinction risk as Least Concern.

B06. ***Boswellia microphylla*** Chiov., Ann. Bot. (Rome) 13: 404. 1915.

Twenty-five occurrence points studied, which we consider sufficient for reliable modelling. The species is restricted to *Acacia-Commiphora* woodland and bushland proper in southern and southeastern Ethiopia, with slight transgressions into transitional semi-evergreen bushland, semi-desert scrubland and desert, and also into saline wetlands (Fig. 8).

There is good agreement between the recorded distribution and areas of highest suitability. The modelled omission rates of *B. microphylla* deviate from the expected values, and the model may not perform as intended. The highest contribution to the model is provided by Bio4 (temperature seasonality).

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* wooded grassland and bushland, usually on red sandy to gravelly soil overlying limestone (Vollesen 1989). In Tropical East Africa (Kenya), it has been found growing in open or dense *Acacia-Commiphora* bushland on stony ridges or slopes or on red sandy soil (Gillett 1991). Thulin (1999) considered *B. neglecta* and *B. microphylla* as one variable species, but kept them distinct in Thulin (2020), stating that it grows in *Acacia-Commiphora* woodland and bushland, usually on red sandy soil overlying limestone, but sometimes on rocky ridges or in gypseous or silty soils.

Restricted to Ethiopia, Somalia, and northeastern Kenya. Not red-listed by IUCN. Thulin (2020) preliminarily suggested an assessment of the extinction risk as Least Concern.

C01. ***Commiphora erlangeriana*** Engl., Bot. Jahrb. Syst. 34: 311. 1904.

Seven occurrence points studied. This is not sufficient for reliable modelling, but as far as known, the

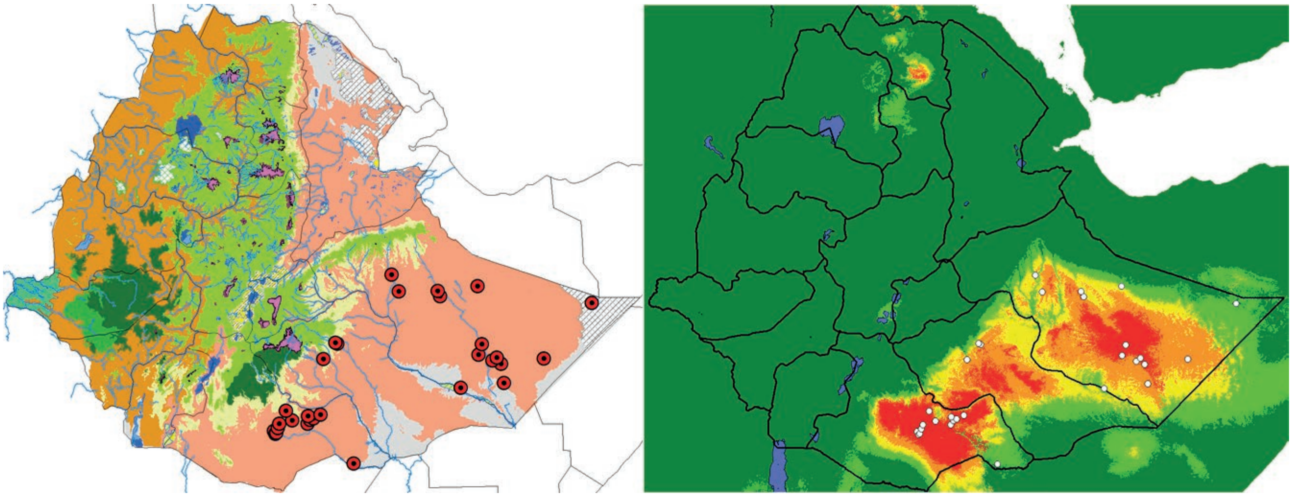


Figure 8. *Boswellia microphylla* Chiov. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see B06.

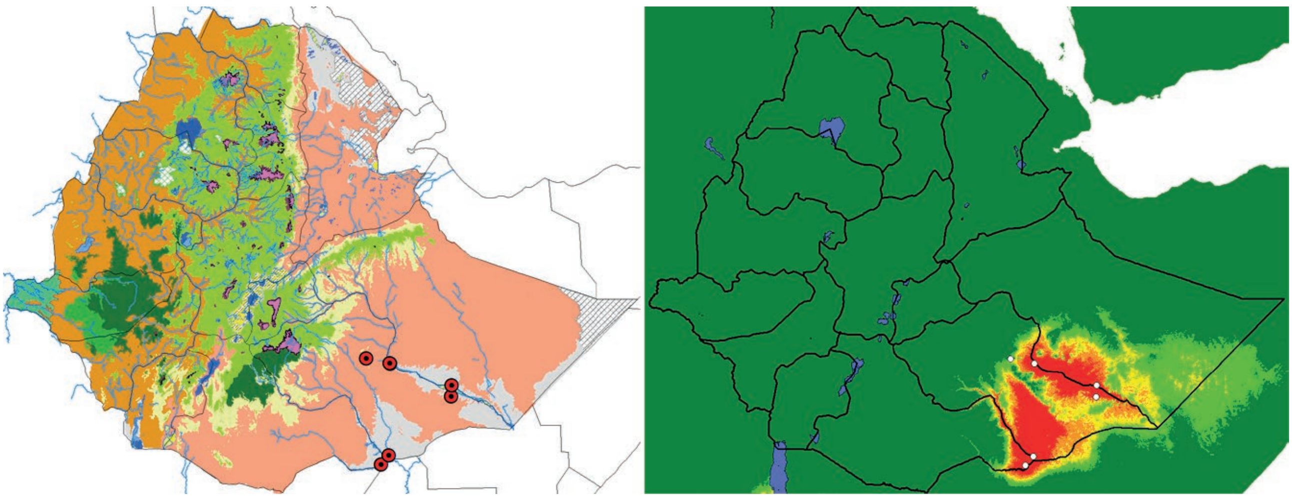


Figure 9. *Commiphora erlangeriana* Engl. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C01.

species is restricted to semi-desert scrublands along or near the lower reach of the Webe Shebele and the Genale rivers, with some transgression into *Acacia-Commiphora* woodland and bushland proper (Fig. 9).

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* bushland on rocky limestone and gypsum slopes (Vollesen 1989). In Tropical East Africa, it was not yet found when the flora was published but it had been collected from hills near the Kenya-Somalia border (Gillett 1991). In Somalia, it has been known from both the northern, central and southern parts, growing in open *Acacia-Commiphora* bushland, usually on gypseous ground (Thulin 1999).

Restricted to Ethiopia and Somalia. The extinction risk of the species is considered Vulnerable B2ab(iii) by Harvey-Brown Y. 2024. *Commiphora erlangeriana*. The IUCN Red List of Threatened Species 2024: e.T231498882A231498888. https://doi.org/10.2305/IUCN.UK.2024-1.RLTS.T231498882A231498888.en. There is a continuing decline in area, extent and/or quality of habitat, and the tree is used for logging and wood harvesting.

C02. ***Commiphora staphyleifolia*** Chiov., Fl. Somala 2: 97. 1932.

One occurrence point studied, and hence the species is not modelled. The only record is from semi-desert scrublands along or near the lower reach of the Genale River (Fig. 10).

In Ethiopia, the species has been reported to grow in open *Acacia-Commiphora* bushland on yellowish alluvium overlying limestone (Vollesen 1989). In Somalia, it has been known from the central and southern part, growing in open bushland on silt plains and on limestone hills (Thulin 1999).

Restricted to Ethiopia and Somalia. This extinction risk of this species is considered Data Deficient by IUCN SSC Global Tree Specialist Group & Botanic Gardens Conservation International (BGCI). 2023. *Commiphora staphyleifolia*. The IUCN Red List of Threatened Species 2023: e.T198161143A198161145. https://doi.org/10.2305/IUCN.UK.2023-1.RLTS.T198161143A198161145.en.

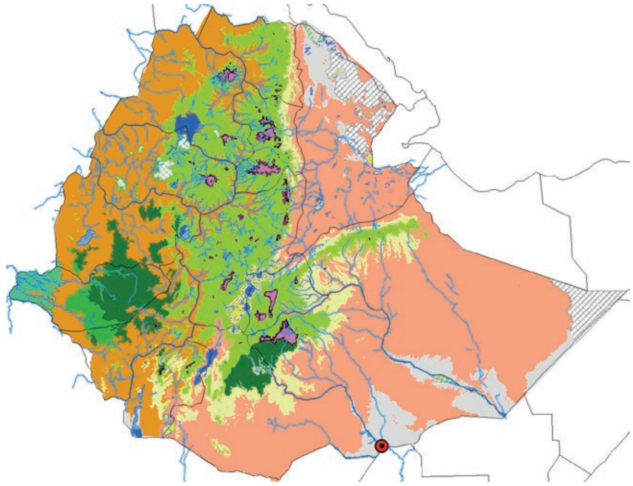


Figure 10. *Commiphora staphyleifolia* Chiov. in Ethiopia. Map showing distribution of observed records on the vegetation types in Fig. 1B. Modelling is not possible based on only one occurrence point. For text about species, see C02.

C03. ***Commiphora unilobata*** J.B.Gillett & Vollesen, Kew Bull. 40: 73. 1985.

Two occurrence points with nearly identical locations have been studied. This is not sufficient for reliable modelling, but as far as is known, the species is restricted to semi-desert scrubland along or near the lower reach of the Genale River (Fig. 11).

In Ethiopia, the species has been reported to grow in open *Acacia-Commiphora* bushland on yellowish alluvium overlying limestone (Vollesen 1989). In Tropical East Africa (Kenya), it has been found in open *Acacia-Commiphora* bushland, chiefly on alluvium (Gillett 1991).

In Somalia, it has been known from the central and southern part, growing in *Acacia-Commiphora* bushland or on silt plains (Thulin 1999).

In Ethiopia, Somalia, northern and eastern Kenya. The extinction risk of the species is considered Near Threatened by Thulin M. 1998. *Commiphora unilobata*. The IUCN Red List of Threatened Species 1998: e.T35166A9915779. https://doi.org/10.2305/IUCN.

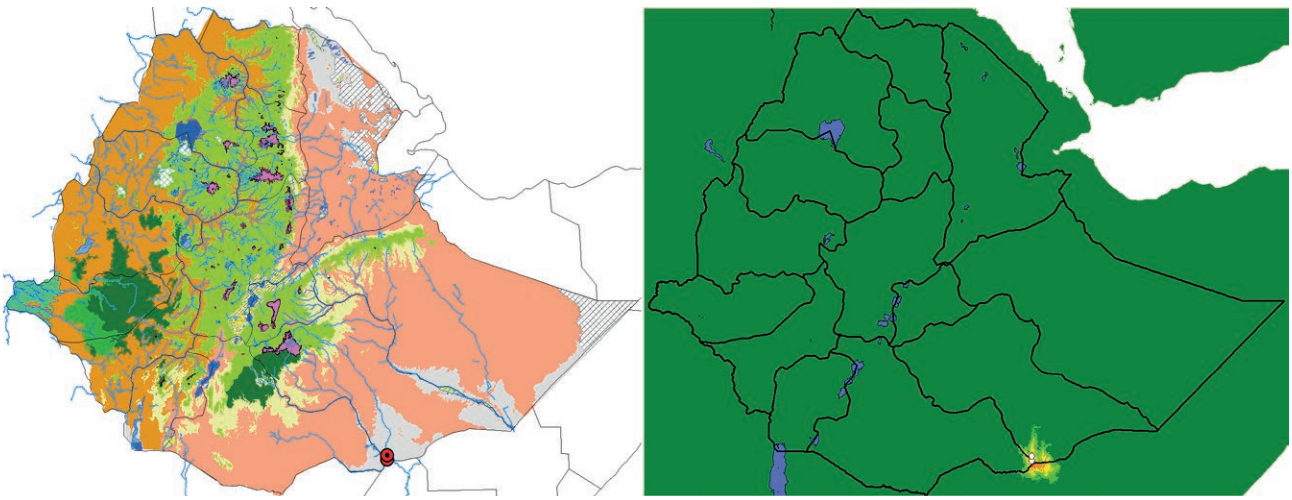


Figure 11. *Commiphora unilobata* Gillett & Vollesen in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C03.

UK.1998.RLTS.T35166A9915779.en. There is a continuing decline in area, extent and/or quality of habitat, and the tree is used for logging and wood harvesting.

C04. ***Commiphora guidottii*** Chiov., Fl. Somala 2: 91. 1932.

(-) *Commiphora guidottii* Chiov. ex Guid., Rivista Ital. Essenze e Profumi 13: 232. 1931, not validly published.

(=) *C. sessiliflora* Vollesen, Kew Bull. 40: 71. 1985.

Eleven occurrence points studied. This is not sufficient for reliable modelling, and the records studied do far from fill the climatic model. Most records are from semi-desert scrublands or *Acacia-Commiphora* bushland along or near the lower reaches of the Genale and Webe Shebele rivers; one record has transgressed into transitional semi-evergreen bushland (Fig. 12).

In Ethiopia, the species has been reported to grow in open to dense *Acacia-Commiphora-Boswellia rivae* bushland on stony slopes with gypseous soils or yellowish alluvium overlying limestone (Vollesen 1989). In Tropical East Africa it was not yet found when the flora was published but it had been collected from hills near the Kenya-Somalia border (Gillett 1991). In Somalia, it has been known from both the northern, central and southern parts, growing in open *Acacia-Commiphora* bushland on gypsum (Thulin 1999).

Restricted to Ethiopia and Somalia. The extinction risk of the species is considered Vulnerable A2c; C1 by Alemu S, Alemu S, Atnafu H, Awas T, Bahdon J, Belay B, Demissew S, Luke WRQ, Mekbib E, Nemomissa S. 2021. *Commiphora guidottii* (errata version published in 2022). The IUCN Red List of Threatened Species 2021: e.T35815A223073528. https://doi.org/10.2305/IUCN.UK.2021-3.RLTS.T35815A223073528.en. There is a continuing decline of mature individuals, a continuing decline in area, extent and/or quality of habitat, and material of the plant is gathered.

In some nomenclatural databases (for example https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:127676-1) the name of this species is stated to have been validly published as the name of a new species by Guidotti (1931: 232) with the intended diagnostic statement "*Pianta a portamento cespuglioso, caratteristica per i rami rivolti verso terra nella parte terminale*." Being published before 1 January 1935, a diagnosis in Italian is sufficient for valid publication of the name for a new species, but Guidotti's statement cannot be a diagnosis distinguishing the new species from other taxa, as required by Turland et. al. (2018: Art. 38.2), because several other shrubs of *Commiphora* in that paper have "branches pointing towards the ground at the end", a fact which in the same paper is documented with habitat photographs of other species of *Commiphora*. We consider Chiovenda's publication from 1932 as the correct place of validation of this name.

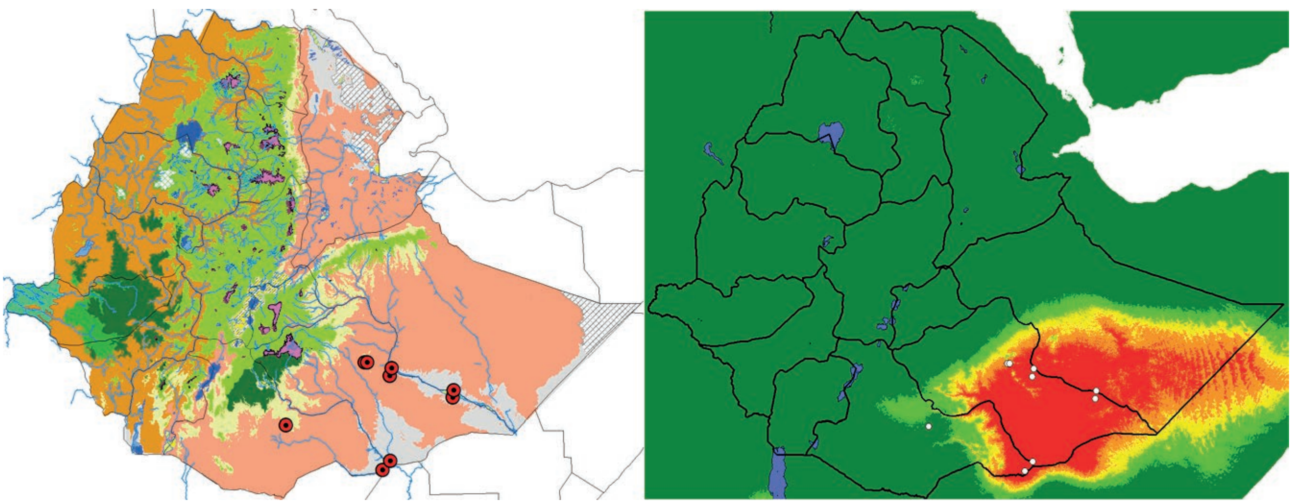


Figure 12. *Commiphora guidottii* Chiov. ex Guid. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. The westernmost outlying collection in SD was included in the modelling but is not in the predicted area. For text about species, see C04.

C05. ***Commiphora paolii*** Chiov., Res. Sci. Somalia Ital. 1: 46. 1916.

(=) *C. longipedicellata* Vollesen, Kew Bull. 40: 69. 1985.

Four occurrence points studied. This is not sufficient for reliable modelling, and the few records do not fill the climatic model. The records studied are from semi-desert scrublands or *Acacia-Commiphora* bushland along or near the lower reach of the Webe Shebele River and a tributary (Fig. 13).

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* bushland on rocky limestone slopes (Vollesen 1989). In Tropical East Africa (Kenya), it has been found growing in *Acacia-Commiphora* bushland and coastal thickets on sand dunes (Gillett 1991). In Somalia, it has been known from the central and southern parts, growing in *Acacia-Commiphora* bushland (Thulin 1999).

Restricted to Ethiopia, Somalia, and northeastern Kenya. Not red-listed by IUCN.

C06. ***Commiphora edulis*** (Klotzsch) Engl. subsp. ***boiviniana*** (Engl.) J.B.Gillett, Fl. Trop. E. Africa, Burserac.: 65. 1991.

(≡) *C. boiviniana* Engl. in A.L.P.P. de Candolle & A.C.P. de Candolle, Monogr. Phan. 4: 21. 1883.

Twelve occurrence points studied. This is not fully sufficient for reliable modelling. The records studied are from varied vegetation around the northern end of Lake Turkana, including *Combretum-Terminalia* woodland, *Acacia-Commiphora* bushland proper, and transitional semi-evergreen bushland (Fig. 14).

There is good agreement between the recorded distribution in Ethiopia and area of highest suitability. However, one southeastern record is far outside the predicted area of distribution. The modelled omission rates of subsp. *boiviniana* are deviating from the expected value, suggesting that the model may not perform as intended. The highest contribution to the model is provided by Bio4 (temperature seasonality).

In Ethiopia, subsp. *boiviniana* has been reported to grow in *Acacia-Commiphora* bushland, in *Combretum-Terminalia* wooded grassland and in dry riverine forest (in the western part of the distribution area), and also on rocky slopes or sandy soil derived from basement rocks, and apparently not in limestone areas (Vollesen 1989). In Tropical East Africa (Uganda, Kenya, Tanzania), it (subsp. *boiviniana*) has been found growing in *Acacia-Commiphora* bushland and semi-evergreen bushland (Gillett 1991). In Somalia, subsp. *boiviniana* is known from the southern parts, growing in *Acacia-Commiphora* bushland and deciduous woodland (Thulin 1999).

Subsp. *boiviniana* is restricted to Ethiopia, Somalia, northeastern Uganda, Kenya, Tanzania. Subsp. *edulis* occurs from Tanzania south to Transvaal. Subsp. *holosericea* is restricted to Kenya. The species is not red-listed as a whole, nor is the status of subsp. *boiviniana* assessed as a distinct taxon. The extinction risk of the species *C. edulis* (as subsp. *edulis*) is considered Least Concern by Botanic Gardens Conservation International (BGCI) &

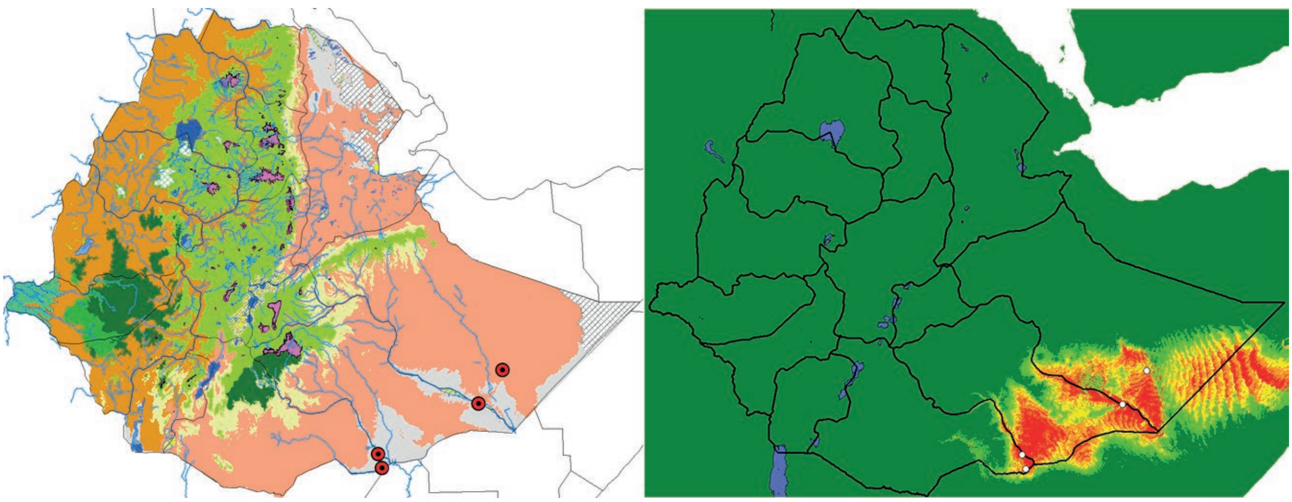


Figure 13. *Commiphora paolii* Chiov. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C05.

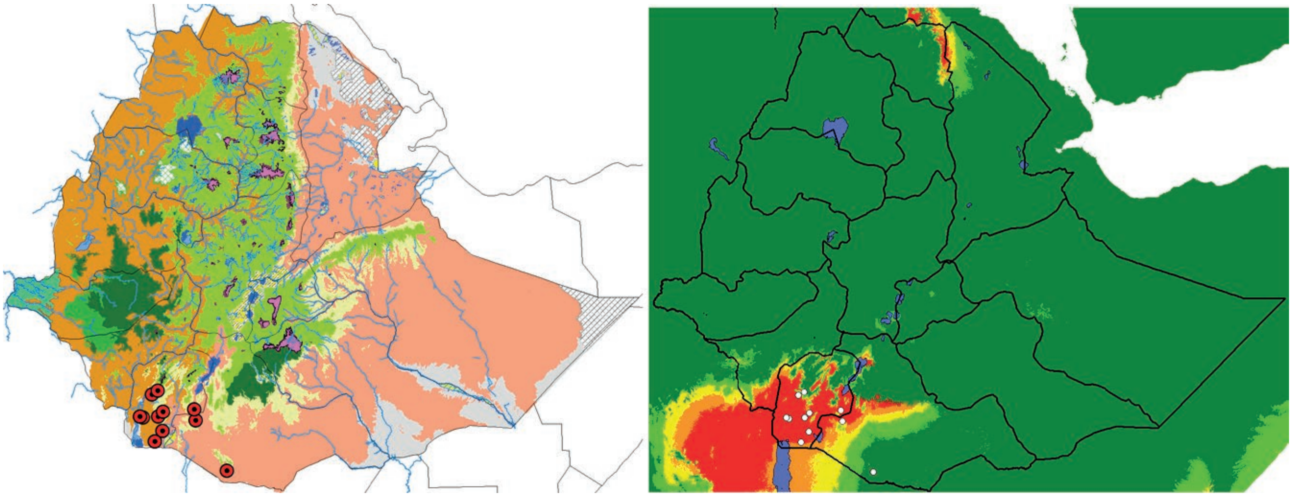


Figure 14. *Commiphora edulis* subsp. *boiviniana* (Engl.) Gillett in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C06.

IUCN SSC Global Tree Specialist Group. 2019. *Commiphora edulis*. The IUCN Red List of Threatened Species 2019: e.T146209364A146209366. https://doi.org/10.2305/IUCN.UK.2019-2.RLTS.T146209364A146209366.en.

C07. ***Commiphora sphaerophylla*** Chiov., Fl. Somala 2: 119. 1932.

(=) *C. ellisiae* Vollesen, Kew Bull. 40: 67. 1985.

Six occurrence points studied. This is not sufficient for reliable modelling, and the six known occurrence points are far apart and do not fill the climatic model. The records studied are from *Acacia-Commiphora* bushland, especially the drier parts of this vegetation type, and a few records are from near semi-desert scrubland at a tributary of the Webe Shebele River (Fig. 15).

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* wooded grassland and bushland on red to brownish sandy soil overlying limestone, and on rocky slopes (Vollesen 1989). In Somalia, it has been known from both northern, central and southern parts, growing in *Acacia-Commiphora* bushland (Thulin 1999).

Restricted to Ethiopia and Somalia. The extinction risk of the species is considered Near Threatened by Thulin M. 1998. *Commiphora sphaerophylla*. The IUCN Red List of Threatened Species 1998: e.T35825A9960461. https://doi.org/10.2305/IUCN.UK.1998.RLTS.T35825A9960461.en.

C08. ***Commiphora myrrha*** (T.Nees) Engl. in A.L.P.P. de Candolle & A.C.P. de Candolle, Monogr. Phan. 4: 10. 1883.

(=) *C. coriacea* Engl., Bot. Jahrb. Syst. 26: 369. 1899.

(=) *C. molmol* (Engl.) Engl. ex Tschirch, Handb. Pharmakogn. 3: 1117. 1925.

(=) *C. cuspidata* Chiov., Bull. Misc. Inform. Kew 1941: 134. 1941.

(=) *C. habessinica* var. *grossedentata* Chiov., Atti Reale Accad. Italia, Mem. Cl. Sci. Fis. 11: 22. 1941.

Thirty-seven occurrence points studied, which we consider sufficient for reliable modelling, and the model has a large distribution area in HA, with smaller areas in SD and BA. However, the records studied are scattered within the areas of highest suitability, including in the southern part of the Afar region. Most records are from *Acacia-Commiphora* bushland proper, but also often collected in semi-desert scrubland along the Genale and the Webe Shebele rivers. Some records have transgressed into transitional semi-evergreen bushland (Fig. 16).

The modelled omission rates of *C. myrrha* agree with the expected values, suggesting that the model may perform as intended. The highest contribution to the model is provided by Bio12 (annual precipitation).

In Ethiopia, the species has been recorded to grow in *Acacia-Commiphora* woodland and bushland on sandy to loamy soil overlying limestone and granite, and

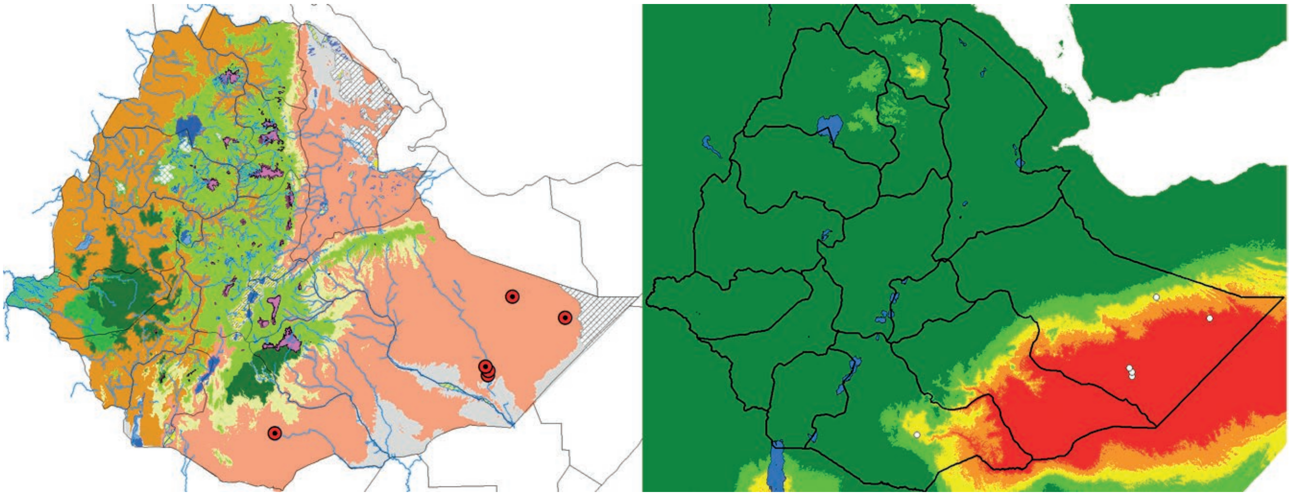


Figure 15. *Commiphora sphaerophylla* Chiov. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C07.

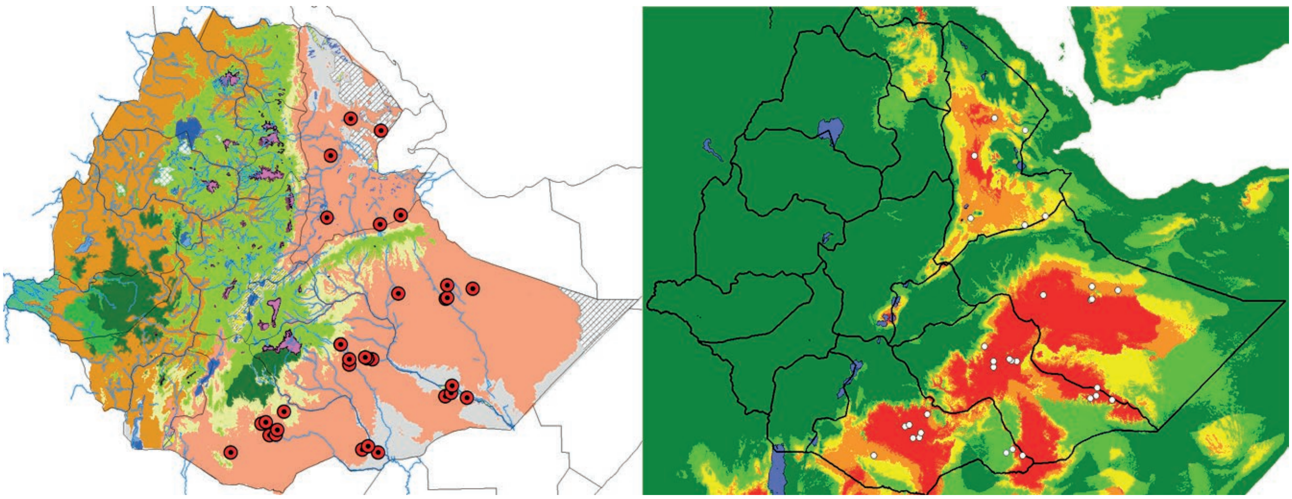


Figure 16. *Commiphora myrrha* (Nees) Engl. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C08.

rocky lava hills (Vollesen 1989). In Tropical East Africa (Kenya), it has been found growing in open *Acacia-Commiphora* bushland in shallow soil over limestone (Gillett 1991). In Somalia, it has been known from both northern, central and southern parts, growing in *Acacia-Commiphora* bushland (Thulin 1999).

In Ethiopia, Somalia, northeastern Kenya, Arabia. Not red-listed by IUCN.

C09. ***Commiphora samharensis*** Schweinf., Bull. Herb. Boissier 7 (App. 2): 290. 1899.

(=) *C. terebinthina* Vollesen, Kew Bull. 40: 45. 1985.

(=) *C. samharensis* subsp. *terebintha* (Vollesen) J.B.Gillett, Fl. Trop. E. Africa, Burserac.: 40. 1991.

Thirty-one occurrence points studied, which we consider sufficient for reliable modelling. However, in spite of the species occurring in Eritrea, the records

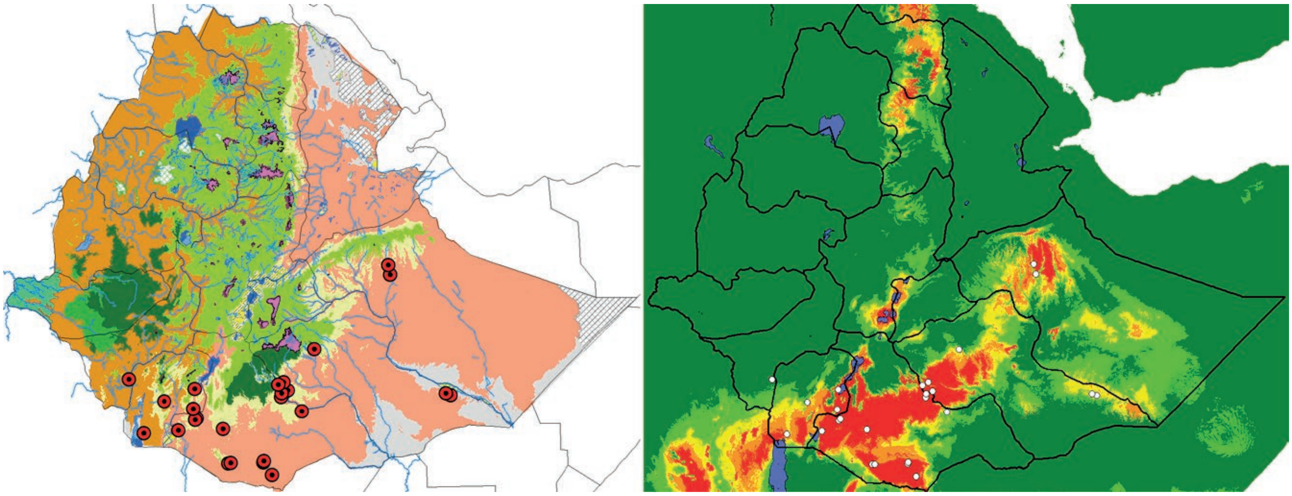


Figure 17. *Commiphora samharensis* Schweinf. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C09.

studied from Ethiopia are scattered within the southern areas with highest suitability, with no records from northern Ethiopia near the long-established records from Eritrea. The species does not fill the suitable climatic area well and has not been recorded from the suitable areas on the eastern escarpment of the Ethiopian highlands in the north. The records are most prominent in GG, SD, and BA, less prominent in HA. Most records are from *Acacia-Commiphora* bushland proper, but the species has also been collected from semi-desert scrubland along the Webe Shebele River, and some records have transgressed into transitional semi-evergreen bushland (Fig. 17).

The modelled omission rates of *C. samharensis* agree with the expected values, suggesting that the model performs as intended. The highest contribution to the model is provided by Bio3 (isothermality).

In Ethiopia, *C. samharensis* has been recorded to grow on rocky hills (Vollesen 1989), but these records are mainly from Eritrea, while the plants from Ethiopia, called *C. terebinthina*, are found widespread in *Acacia-Commiphora* woodland and bushland in southern Ethiopia, as well as in wooded grassland, *Combretum-Terminalia* wooded grassland, all on whitish to red sandy to stony soil overlying limestone or basement rocks, on rocky slopes and on black cotton soil (Vollesen 1989). In Tropical East Africa (Uganda, Kenya, Tanzania), it has been found growing in *Acacia-Commiphora* bushland and bushed grassland (Gillett 1991). In Somalia, it has been known from both northern, central and southern parts, growing in *Acacia-Commiphora* bushland and wooded grassland (Thulin 1999).

The species is widespread in eastern Sudan (Darbyshire et al. 2015), Eritrea, Ethiopia, Somalia, northeastern Uganda, Kenya, and northeastern Tanzania. Not red-listed by IUCN.

C10. ***Commiphora schimperi*** (O.Berg) Engl. in A.L.P.P. de Candolle & A.C.P. de Candolle, Monogr. Phan. 4: 13. 1883.

(=) *C. arussensis* Engl., Bot. Jahrb. Syst. 34(3): 305. 1904.

Forty-three occurrence points studied, which we consider sufficient for reliable modelling. Most records are from *Acacia-Commiphora* bushland proper, but the species also occur in *Combretum-Terminalia* woodland in the deep values of rivers running westwards towards the Nile, as well as in *Acacia* wooded grassland of the Rift Valley (Fig. 18).

The records studied are widely scattered within the southern areas with highest suitability, particularly in southern Ethiopia, but the records only fill the suitable climatic areas moderately well outside southern Ethiopia. The modelled omission rates of *C. schimperi* agree with the expected values, suggesting that the model performs as intended. The highest contribution to the model is provided by Bio14 (precipitation of driest month).

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora*, *Acacia-Combretum* and *Combretum-Terminalia* woodland and bushland, on red sandy to stony soil overlying limestone and basement rocks, also on rocky slopes, on black cotton soil and ter-

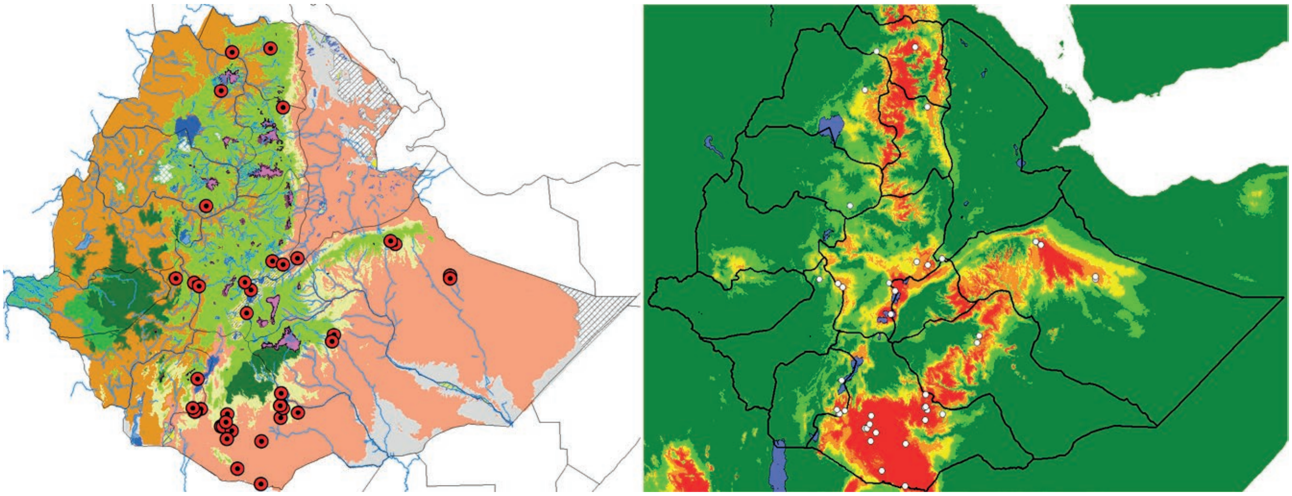


Figure 18. *Commiphora schimperi* (Berg) Engl. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C10.

mite mounds (Vollesen 1989). In Tropical East Africa (Uganda, Kenya, Tanzania), it has been found growing in bushed grassland and *Acacia-Commiphora* bushland (Gillett 1991). In Somalia, it has been known from both northern, central and southern parts, growing in *Acacia-Commiphora* bushland and woodland (Thulin 1999).

The species is widespread in Sudan (Darbyshire et al. 2015), Somalia, Uganda, Kenya, Tanzania, and southwards to South Africa; also in Arabia. The extinction risk of the species is considered Least Concern by Botanic Gardens Conservation International (BGCI) & IUCN SSC Global Tree Specialist Group. 2021. *Commiphora schimperi* (amended version of 2020 assessment). The IUCN Red List of Threatened Species 2021: e.T88322531A208439214. https://doi.org/10.2305/IUCN.UK.2021-3.RLTS.T88322531A208439214.en. The status of the species is considered stable.

C11. ***Commiphora obovata*** Chiov., Bull. Misc. Inform. Kew 1941: 136. 1941.

Four occurrence points studied. This is not sufficient for reliable modelling, and the few records do far from fill the climatic model. The records studied are widely scattered in *Acacia-Commiphora* bushland, and some are transgressing into transitional semi-evergreen bushland (Fig. 19).

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* bushland on rocky limestone slopes (Vollesen 1989). In Tropical East Africa (Kenya), it has been found growing in broken and scattered semi-evergreen coastal bushland (Gillette 1991). In Somalia, it has been known from the northern and central parts, growing in *Acacia-Commiphora* bushland (Thulin 1999).

Restricted to Ethiopia, Somalia, and Kenya. The extinction risk of the species is considered Near Threatened by Thulin M. 1998. *Commiphora obovata*. The IUCN Red List of Threatened Species 1998: e.T34799A9885922. https://doi.org/10.2305/IUCN.UK.1998.RLTS.T34799A9885922.en. The status is considered in need of updating.

C12. ***Commiphora africana*** (A.Rich.) Engl. in A.L.P.P. de Candolle & A.C.P. de Candolle, Monogr. Phan. 4: 14. 1883.

(=) *C. tubuk* Sprague in Hooker's Icon. Pl. 32: t. 3108. 1927.

Ninety-five occurrence points have been studied, which we consider sufficient for reliable modelling. In particular, the records studied are scattered within the southern areas with highest suitability but are widely scattered in other parts of the areas predicted to be suitable, including in the deep valley of rivers in the south running towards the Nile in the northwest and west, towards Lake Turkana in the south, to the Webe Shebele in the southeast, and to the Awash River basin in the east.

Most records are from *Acacia-Commiphora* bushland proper, but the species has also been collected from *Combretum-Terminalia* woodland in the southwest and the northeast, as well as close to semi-desert scrubland

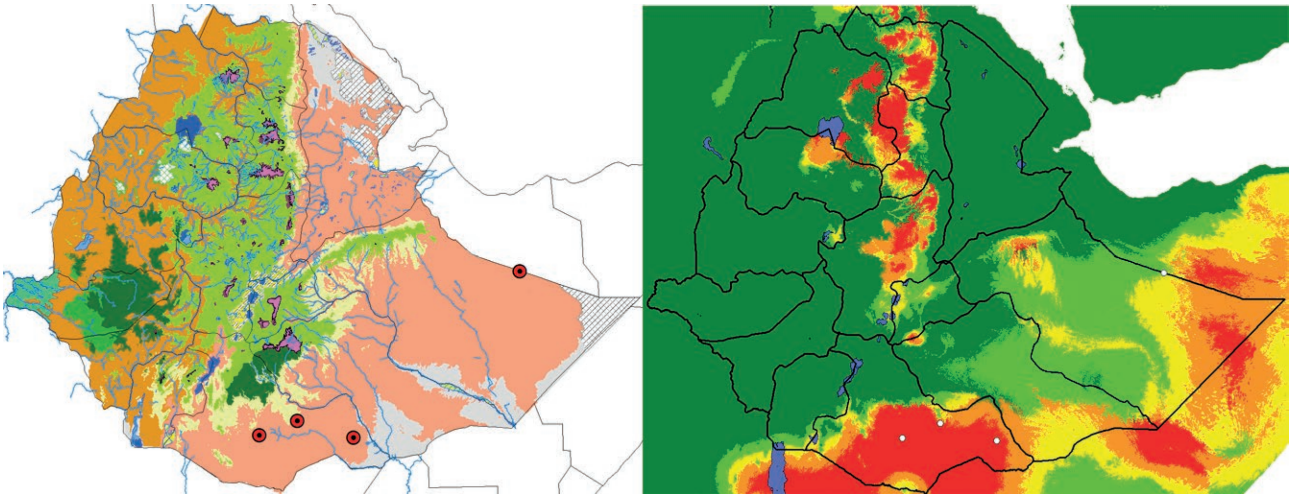


Figure 19. *Commiphora obovata* Chiov. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. Large areas in northern Ethiopia are predicted to have climatically suitable areas for the species, but it has not been found there. For text about species, see C11.

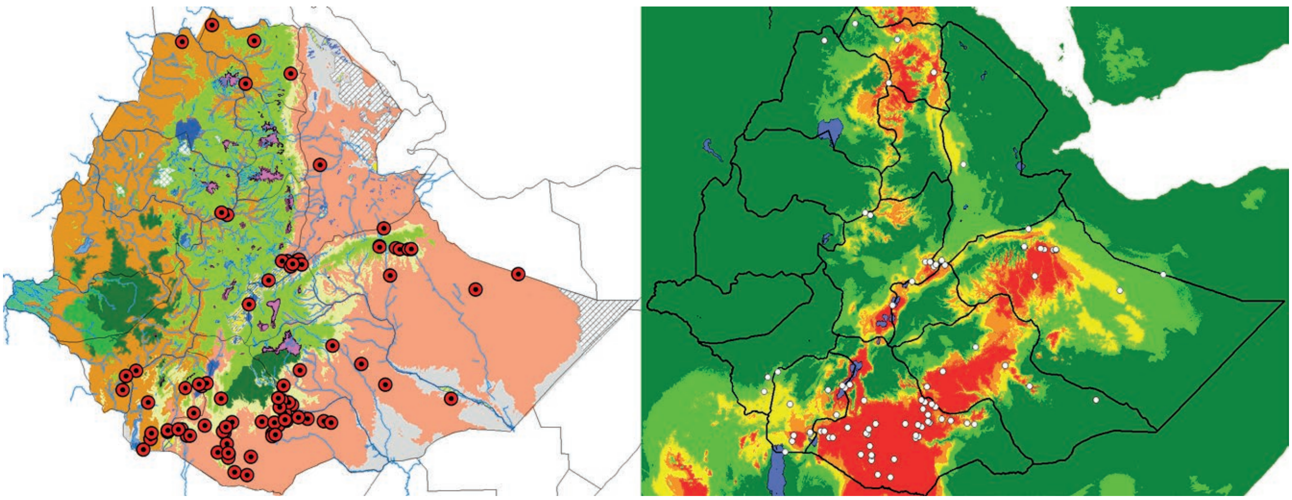


Figure 20. *Commiphora africana* (A. Rich.) Engl. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. One southeastern record is outside the predicted area. For text about species, see C12.

at the Webe Shebele River, and it transgresses into transitional semi-evergreen bushland (Fig. 20).

The modelled omission rates of *C. africana* agree with the expected values, suggesting that the model performs as intended. The highest contribution to the model is provided by Bio3 (isothermality).

In Ethiopia, the species has been reported to grow in *Acacia* and *Acacia-Commiphora* bushland, *Commiphora-Boswellia*, *Acacia-Terminalia*, *Acacia-Balanites*, and *Combretum-Terminalia* woodland, wooded grassland and bushland, often on rocky slopes in areas with basement rocks but also on level sandy to loamy soil and recent lava flows. This summary is based on the combined information about *C. africana* and *C. tubuk* in Vollesen (1989).

In Tropical East Africa (Uganda, Kenya, Tanzania), it has been found to be very variable and reported to grow in bushed grassland, *Acacia-Commiphora* bushland, in dry open *Acacia-Commiphora* bushland and in coastal semi-evergreen thickets (Gillett 1991). In Somalia, it has been known from northern, central and southern parts, growing in *Acacia-Commiphora* bushland or woodland, also on sand of coastal dunes (Thulin 1999).

The species is widespread in drier parts of Africa from Senegal to Sudan (Darbyshire et al. 2015) and Ethiopia and south to Namibia, Zimbabwe, and Mozambique. The extinction risk of the species is considered Least Concern by Botanic Gardens Conservation International (BGCI) & IUCN SSC Global Tree Specialist Group. 2019. *Commiphora africana*. The IUCN Red List of Threatened Species 2019: e.T146216386A146216388. https://doi.org/10.2305/IUCN.UK.2019-2.RLTS.T146216386A146216388.en. The status of the species is considered stable.

C13. ***Commiphora monoica*** Vollesen, Kew Bull. 40: 62. 1985.

Seven occurrence points in three locations studied. The species is endemic to Ethiopia, and we have to consider seven records sufficient for modelling. These few records do far from fill the climatic model, with a much smaller recorded distribution in the south than predicted, and there are no records in highly suitable areas in the north (Fig. 21).

The records studied are all from transitional semi-evergreen bushland in the south. In its restricted area the species has been recorded from dense *Commiphora* woodland on rocky limestone slopes and *Acacia-Commiphora* bushland on black cotton soil (Vollesen 1989).

The species is endemic to Ethiopia. The extinction risk of the species is considered Critically Endangered B1ab(i,ii,iii,iv,v); C2a(i,ii) by D. Alemu S, Alemu S, Atnafu H, Awas T, Belay B, Demissew S, Luke WRQ, Mekbib E, Nemomissa S. 2021. *Commiphora monoica* (errata version published in 2022). The IUCN Red List of Threatened Species 2021: e.T34389A223071378. https://doi.org/10.2305/IUCN.UK.2021-3.RLTS.T34389A223071378.en. There is a continuing decline in number of mature individuals, in area, extent and/or quality of habitat, and material is being collected from the wild.

C14. ***Commiphora pedunculata*** (Kotschy & Peyr.) Engl. in A.L.P.P. de Candolle & A.C.P. de Candolle, Monogr. Phan. 4: 23. 1883.

Eleven occurrence points studied. This is not sufficient for reliable modelling, but the few records from the western border of Ethiopia fill one of two highly suitable areas in *Combretum-Terminalia* woodland in western Ethiopia, forming the eastern end of the total distribution area of the species (Fig. 22).

In Ethiopia, according to Vollesen (1989), the species was expected to grow in *Combretum-Terminalia* woodland and wooded grassland, but this was not based on material from inside Ethiopia. However, the information has been confirmed from detailed studies in the field by Friis et al. (2022). In Tropical East Africa (southwestern Tanzania), it has been found growing in *Brachystegia* woodland and in mixed deciduous woodland (Gillett 1991).

The species is widespread from Mali to Sudan, South Sudan (Darbyshire et al. 2015), and W Ethiopia, south to southern Tanzania, Malawi and Zambia. The

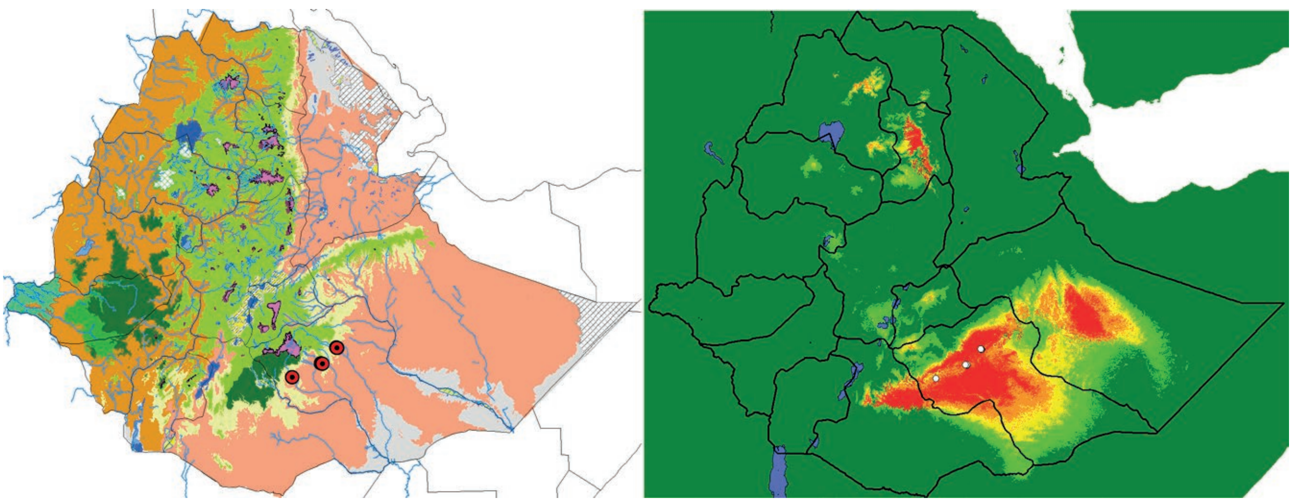


Figure 21. *Commiphora monoica* Vollesen in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C13.

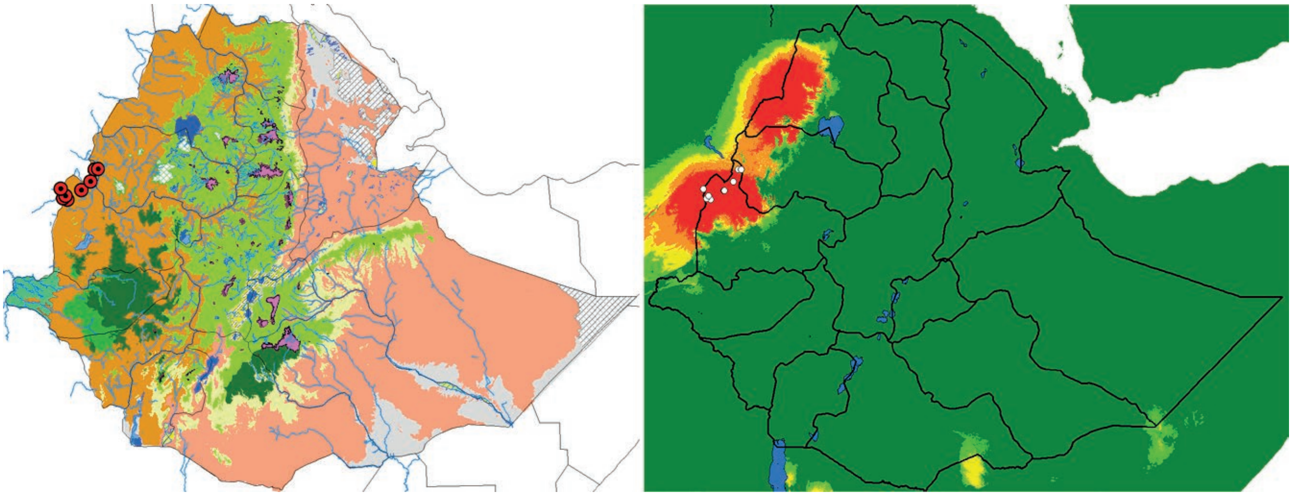


Figure 22. *Commiphora pedunculata* (Kotschy & Peyr.) Engl. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C14.

extinction risk of the species is considered Least Concern by Botanic Gardens Conservation International (BGCI) & IUCN SSC Global Tree Specialist Group. 2018. *Commiphora pedunculata*. The IUCN Red List of Threatened Species 2018: e.T128045009A135814518. https://doi.org/10.2305/IUCN.UK.2018-2.RLTS.T128045009A135814518.en. The status of the species and habitat is considered stable.

C15. ***Commiphora hildebrandtii*** Engl. in A.L.P.P. de Candolle & A.C.P. de Candolle, Monogr. Phan. 4: 15. 1883.

Nine occurrence points studied. This is not sufficient for reliable modelling, and the few records do far from fill the climatic model, with a scattered recorded distribution in the south that does not fill the highly suitable areas as predicted, and there are no records in the highly suitable area in the north. The records studied are all scattered in *Acacia-Commiphora* bushland proper, but marginal to transitional semi-evergreen bushland (Fig. 23).

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* woodland, wooded grassland and bushland on rocky limestone slopes and ridges (Vollesen 1989). In Thulin (1999) *C. hildebrandtii* and *C. ogadensis* were considered conspecific, and therefore no information was given other than the species grow in *Acacia-Commiphora* bushland.

Restricted to Ethiopia and Somalia. The extinction risk of the species is considered Least Concern by Alemu S, Alemu S, Atnafu H, Awas T, Belay B, Demissew S, Luke WRQ, Mekbib E, Nemomissa S. 2021. *Commiphora hildebrandtii* (errata version published in 2022). The IUCN Red List of Threatened Species 2021: e.T128044736A223075194. https://doi.org/10.2305/IUCN.UK.2021-3.RLTS.T128044736A223075194.en. The trends in population size and habitat are unknown.

C16. ***Commiphora ogadensis*** Chiov., Fl. Somala 2: 103. 1932.

Eight occurrence points studied. This is not sufficient for reliable modelling, and the few records do far from filling the climatic model, with a very scattered distribution recorded in the south. The species has been recorded from the *Acacia-Commiphora* bushland proper, but more records are from the transitional semi-evergreen bushland (Fig. 24).

No records have been observed from the areas with high or highest suitability in northern Ethiopia.

In Ethiopia, the species has been recorded to grow in *Acacia-Commiphora* woodland and bushland, on red sandy soil overlying limestone, on black cotton soil and, and on soil derived from granitic rocks (Vollesen 1989). In Tropical East Africa (Kenya), it has been found growing in *Acacia-Commiphora* bushland on alluvial soil, usually near base of mountains (Gillett 1991).

In Thulin (1999), *C. hildebrandtii* and *C. ogadensis* were considered conspecific, and therefore no information was given other than that the species grows in *Acacia-Commiphora* bushland.

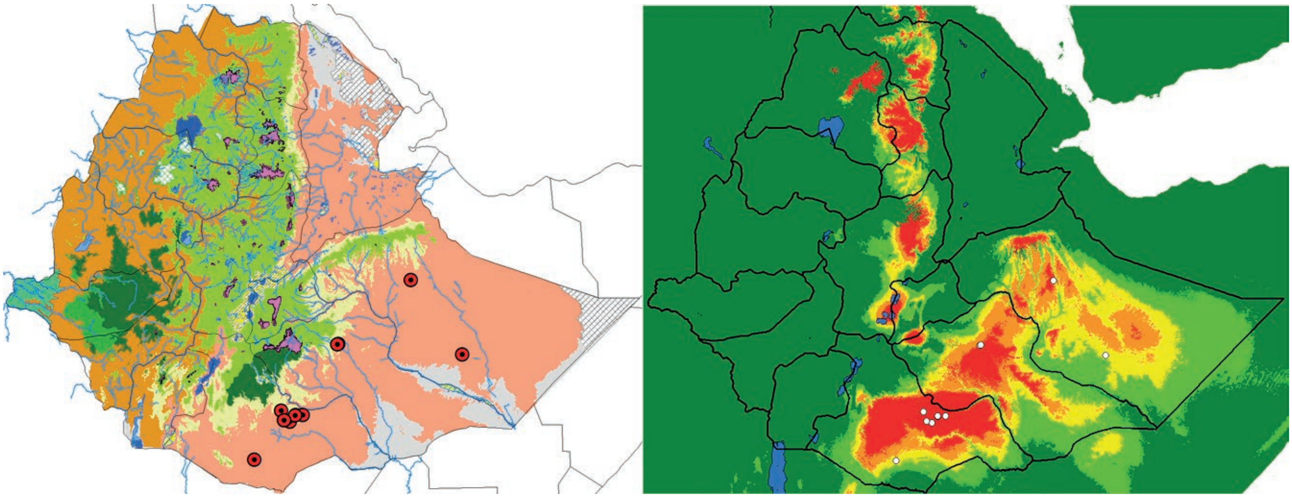


Figure 23. *Commiphora hildebrandtii* (Engl.) Engl. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C15.

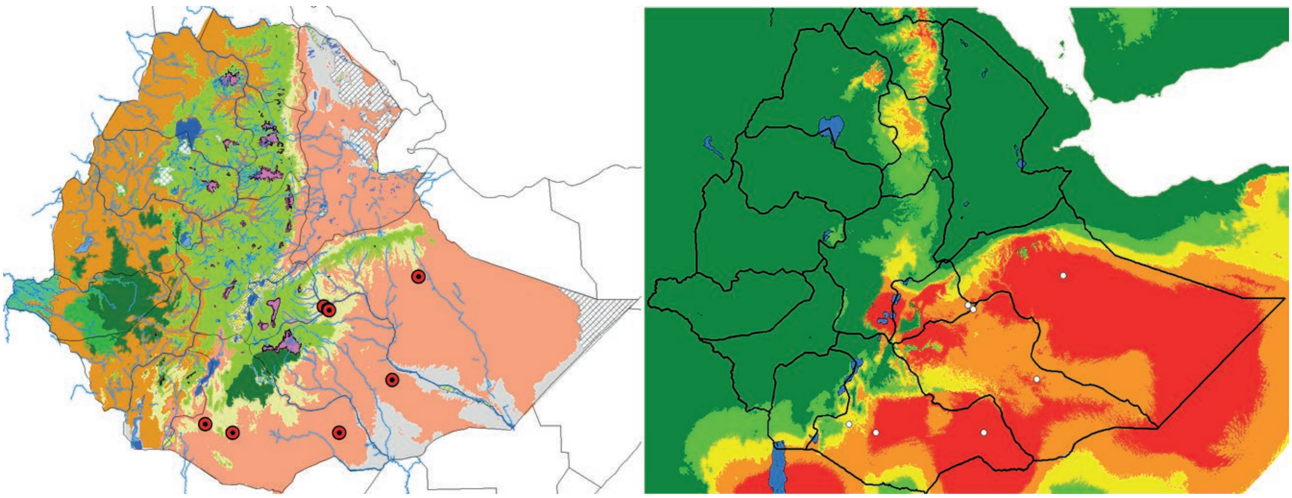


Figure 24. *Commiphora ogadensis* Chiov. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C16.

Restricted to Ethiopia, Somalia, and northeastern Kenya. The extinction risk of the species is considered Data Deficient by Alemu S, Alemu S, Atnafu H, Awas T, Belay B, Demissew S, Luke WRQ, Musili P, Nemomissa S, Bahdon J, Mekbib E. 2021. *Commiphora ogadensis* (errata version published in 2022). The IUCN Red List of Threatened Species 2021: e.T133268514A223078443. https://doi.org/10.2305/IUCN.UK.2021-3.RLTS.T133268514A223078443.en. The trends in population size and habitat are unknown.

C17. ***Commiphora corrugata*** J.B.Gillett & Vollesen, Kew Bull. 40: 59. 1985.

Twenty-seven occurrence points studied, which we consider sufficient for reliable modelling. The recorded distribution is scattered within the southeastern parts of Ethiopia with most records from *Acacia-Commiphora* bushland proper, but the species also transgresses into transitional semi-evergreen bushland (Fig. 25).

No records have been observed from the areas with high or highest suitability in northern Ethiopia. The

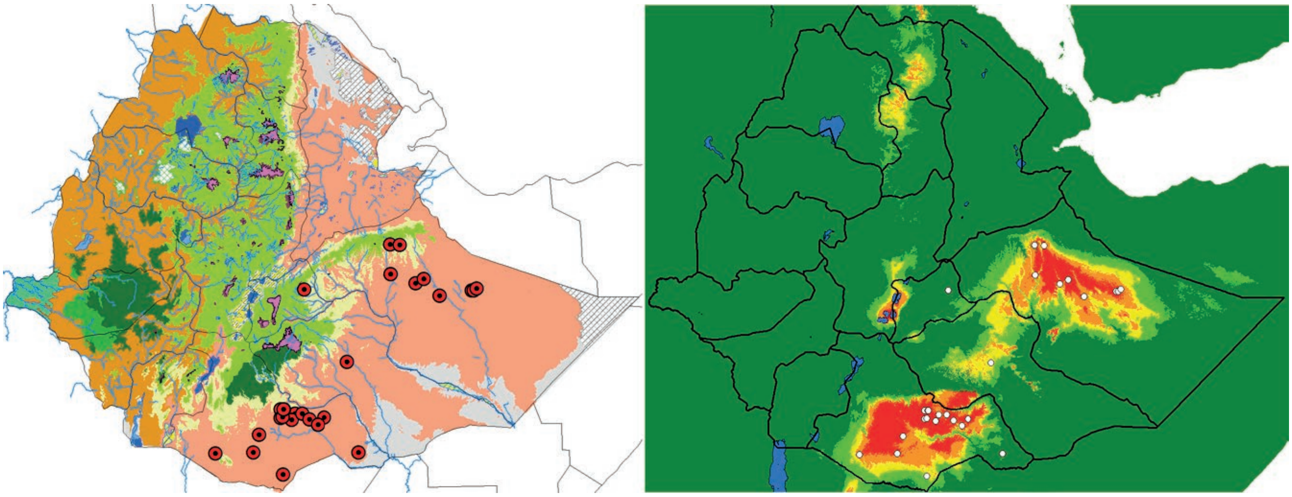


Figure 25. *Commiphora corrugata* Gillett & Vollesen in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C17.

modelled omission rates of *C. corrugata* agree with the expected values, suggesting that the model performs as intended. The highest contribution to the model is provided by Bio3 (isothermality).

In Ethiopia, the species has been recorded to grow in *Acacia-Commiphora* woodland, wooded grassland and bushland on rocky limestone slopes and ridges (Vollesen 1989). In Tropical East Africa (Kenya), it has been found growing in *Acacia-Commiphora* bushland on limestone slopes (Gillett 1991). In Somalia, it is known from the central and southern parts, growing in *Acacia-Commiphora* bushland, usually on limestone (Thulin 1999).

In Ethiopia, Somalia, northeastern Kenya. The extinction risk of the species is considered Near Threatened C1 by Alemu S, Alemu S, Atnafu H, Awas T, Belay B, Demissew S, Luke WRQ, Mekbib E, Nemomissa S. 2021. *Commiphora corrugata* (errata version published in 2022). The IUCN Red List of Threatened Species 2021: e.T35164A223073349. https://doi.org/10.2305/IUCN.UK.2021-3.RLTS.T35164A223073349.en. The population size is declining.

C18. ***Commiphora truncata*** Engl., Bot. Jahrb. Syst. 34: 309. 1904.

Four occurrence points studied. This is not sufficient for reliable modelling, and the few records do far from fill the large area occupied by the climatic model. Three records are from drier parts of *Acacia-Commiphora* bushland proper, while one record is from near semi-desert scrubland at a tributary to the Webe Shebele River (Fig. 26).

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* bushland on red sandy soil to stony soil overlying limestone (Vollesen 1989). In Somalia, it has been found both in the northern, central and southern parts, growing in *Acacia-Commiphora* bushland and semi-desert scrub (Thulin 1999).

Restricted to Ethiopia and Somalia. The extinction risk of the species is considered Near Threatened by Thulin M. 1998. *Commiphora truncata*. The IUCN Red List of Threatened Species 1998: e.T35831A9961055. https://doi.org/10.2305/IUCN.UK.1998.RLTS.T35831A9961055.en. The trends in population size and habitat are unknown.

C19. ***Commiphora confusa*** Vollesen, Kew Bull. 40: 54. 1985.

Twenty-four occurrence points studied, which we consider sufficient for reliable modelling. Most records studies are from *Acacia-Commiphora* bushland proper in southern Ethiopia, but the species also transgresses into *Combretum-Terminalia* woodland to the west of the Omo River and transitional semi-evergreen bushland further to the east; one record is from near the semi-desert scrubland at the Webe Shebele River (Fig. 27).

The records fill the suitable climatic areas in southern Ethiopia, but no records have been observed from the areas with high or highest suitability in northern Ethiopia, and it is striking that such a fairly common species does not seem to have been found in southeastern Ethiopia when it is also common in eastern Kenya.

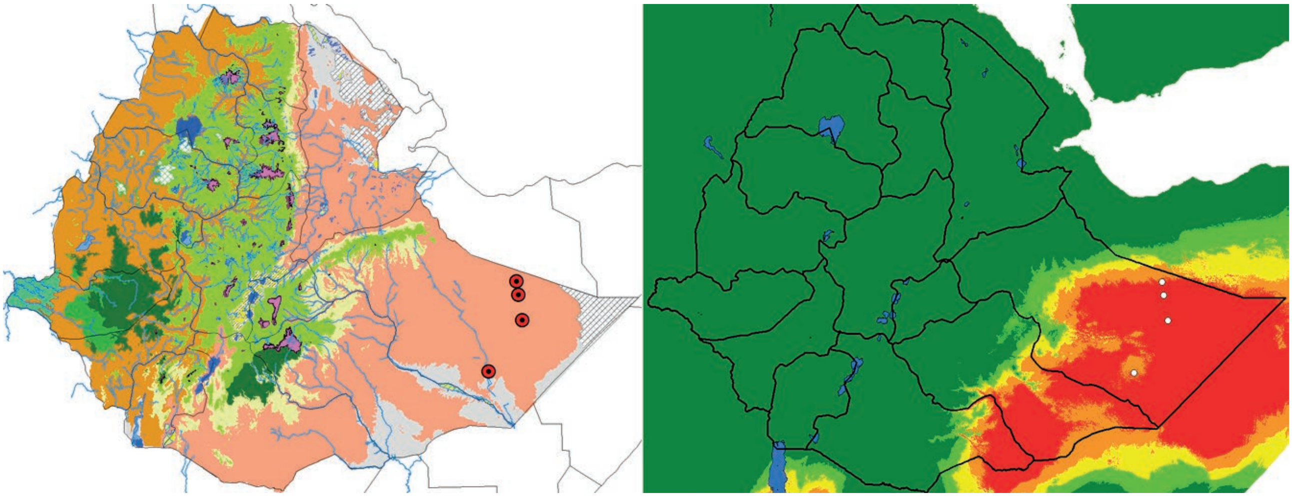


Figure 26. *Commiphora truncata* Engl. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C18.

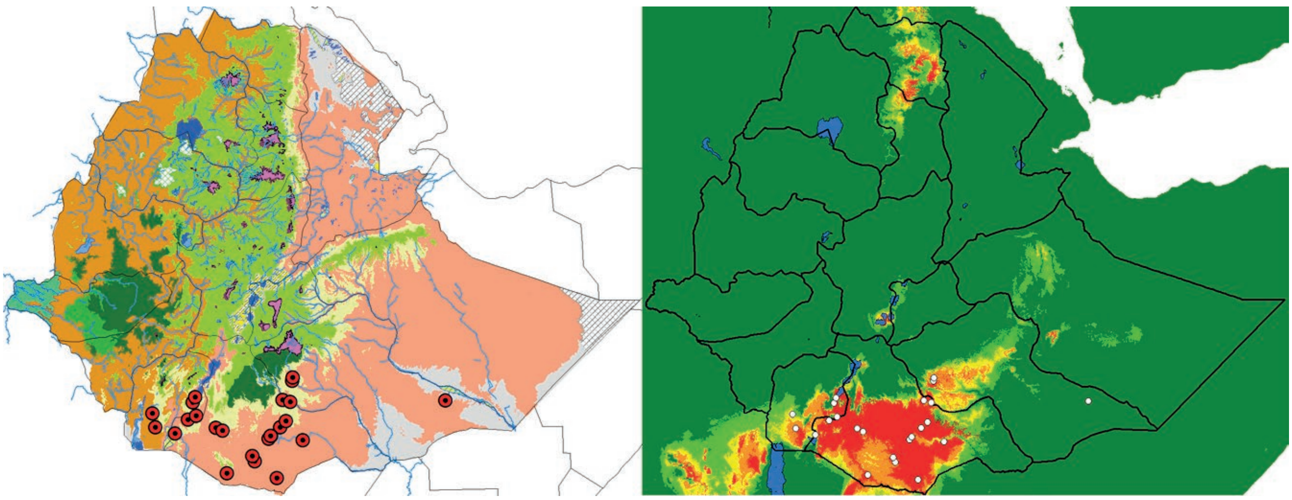


Figure 27. *Commiphora confusa* Vollesen in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. One southeastern record is outside the predicted area. For text about species, see C19.

The modelled omission rates of *C. confusa* agree partly with the expected values, suggesting that the model may perform as intended.

The highest contribution to the model is provided by Bio3 (isothermality).

In Ethiopia, the species has been reported to grow in dense *Acacia-Commiphora* bushland on rocky slopes or grey sandy soil over basement rocks (Vollesen 1989). In Tropical East Africa (Kenya, Tanzania), it has been found growing in *Acacia-Commiphora* bushland (Gillett 1991).

The species is widespread in Ethiopia, recorded from South Sudan (Darbyshire et al. 2015), northern and eastern Kenya, and northeastern Tanzania. The extinction risk of the species is considered Least Concern by Kamau P. 2022. *Commiphora confusa*. The IUCN Red List of Threatened Species 2022: e.T215410196A215570173. https://doi.org/10.2305/IUCN.UK.2022-2.RLTS.T215410196A215570173.en. The population size is declining.

C20. ***Commiphora alaticaulis*** J.B.Gillett & Vollesen, Kew Bull. 40: 52. 1985.

Six occurrence points studied. This is not sufficient for reliable modelling. The Ethiopian records are from localities at different altitudes, and it is best known from the area around Sof Omar in BA. We must conclude that the potential vegetation types, in which *C. alaticaulis* occurs, are *Acacia-Commiphora* bushland proper, transitional semi-evergreen bushland and semi-desert scrub. The potentially modelled area based on climatic parameters is large, and the observed records only fill a small area inside large areas with potentially suitable climate. It seems relevant to study other environmental parameters that might restrict the distribution of this species (Fig. 28).

No records have been observed from the areas with high or highest suitability in northern Ethiopia.

In Ethiopia, the species has been recorded to grow in *Acacia-Commiphora* woodland and bushland on red sandy soil overlying limestone and on rocky limestone slopes (Vollesen 1989). In Tropical East Africa (Kenya), it has been found growing in open *Acacia-Commiphora* bushland (Gillett 1991). In Somalia, it has been found both in northern, central and southern parts, growing in *Acacia-Commiphora* bushland (Thulin 1999).

Restricted to Ethiopia, Somalia, and northeastern Kenya. The extinction risk of the species is considered Vulnerable B2ab(iii) by Harvey-Brown Y. 2022. *Commiphora alaticaulis*. The IUCN Red List of Threatened Species 2022: e.T183102075A183102077. https://doi.org/10.2305/IUCN.UK.2022-2.RLTS.T183102075A183102077.en. The trend in population size is unknown, but there is continuing decline in area, extent and/or quality of habitat.

C21. ***Commiphora kataf*** (Forssk.) Engl. in A.L.P.P. de Candolle & A.C.P. de Candolle, Monogr. Phan. 4: 19. 1883.

(=) *C. erythraea* (Ehrenb.) Engl. in A.L.P.P. de Candolle & A.C.P. de Candolle, Monogr. Phan. 4: 20. 1883.

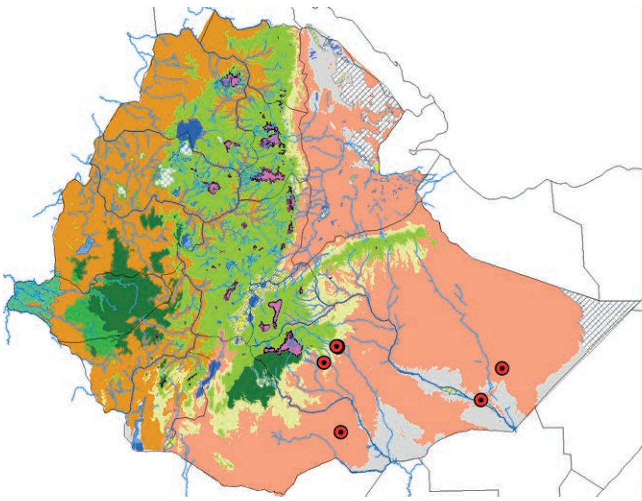
(=) *C. gallaensis* Engl. Engl., Bot. Jahrb. Syst. 48: 487. 1912.

(=) *C. kataf* (Forssk.) Engl. subsp. *turkanensis* J.B.Gillett, Fl. Trop. E. Africa, Burserac.: 81. 1991.

(=) *C. baluensis* Engl., Bot. Jahrb. Syst. 34: 313. 1904.

(=) *C. holtziana* Engl., Bot. Jahrb. Syst. 34: 310. 1904.

Forty-five occurrence points studied, which we consider sufficient for reliable modelling. The records studied are scattered within the areas with highest suitability and the highest density is in southern Ethiopia. Some isolated records are from the southern part of the Afar region. Most records occur in *Acacia-Commiphora* bushland proper, but also often collected in the semi-desert scrubland at the Genale and Webe Shebele rivers, and some records have transgressed into transitional semi-evergreen bushland (Fig. 29).



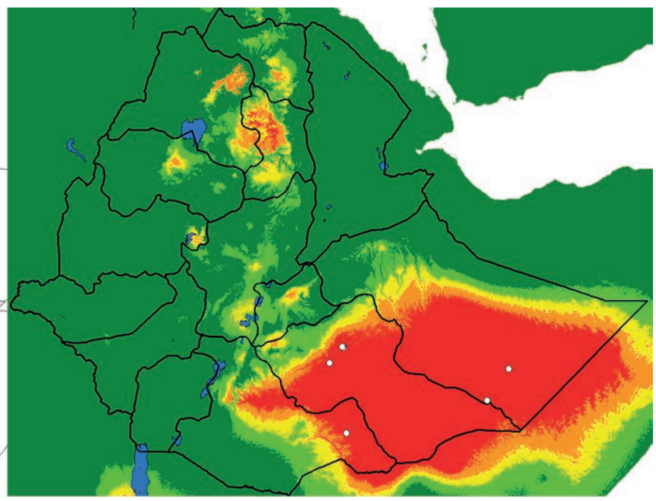


Figure 28. *Commiphora alaticaulis* Gillett & Vollesen in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C20.

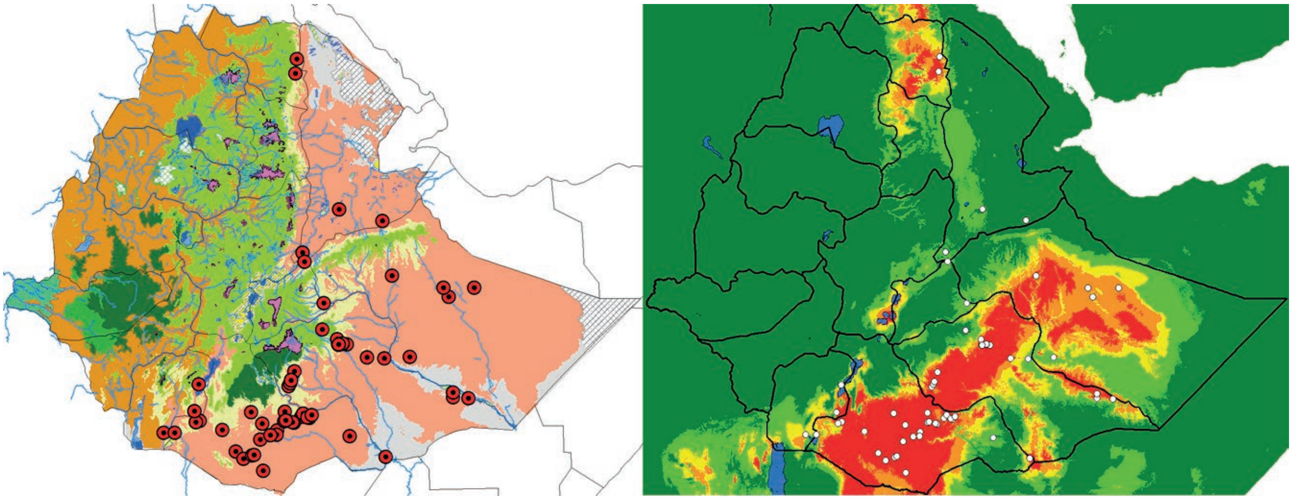


Figure 29. *Commiphora kataf* (Forssk.) Engl. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C21.

No records have been observed from the areas with highest suitability in northern Ethiopia. The modelled omission rates of *C. kataf* agree with the expected values, suggesting that the model performs as intended. The highest contribution to the model is provided by Bio3 (isothermality).

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* woodland and bushland, in *Combretum-Terminalia* wooded grassland [in western part of the distribution area], and on rocky slopes of basement rocks as well as limestone. In Tropical East Africa (Uganda, Kenya, Tanzania), it has been recorded as variable and has been found growing in deciduous woodland, dry forest, *Acacia-Commiphora* bushland on well drained and sandy soils, and on hillsides (Gillett 1991). In Somalia, it has been found to be widespread in northern, central and southern parts, growing in deciduous woodland (Thulin 1999).

The species is widespread in Ethiopia, Eritrea, northeastern Sudan (Darbyshire et al. 2015), Somalia, Kenya, and northern Tanzania; also in Arabia. It has not been red-listed as a species of this name, but the extinction risk of the taxon carrying the synonym *C. baluensis* is considered Least Concern by Beentje HJ. 2022. *Commiphora baluensis*. The IUCN Red List of Threatened Species 2022: e.T214701672A214702915. https://doi.org/10.2305/IUCN.UK.2022-2.RLTS.T214701672A214702915.en. The extinction risk of the taxon carrying the synonym *C. holtziana* is also considered Least Concern by Beentje HJ, Gereau RE, Hilton-Taylor C, Howard G, Kindeketa W, Luke WRQ, Maunder M, Mwachala G, Mwangoka M, Ndangalasi H, Njau E-F, Schatz GE, Siro Masinde P, Wilkins VL. 2020. *Commiphora holtziana*. The IUCN Red List of Threatened Species 2020: e.T158137A762492. https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T158137A762492.en.

C22. ***Commiphora rostrata*** Engl., Ann. Bot. (Rome) 7: 17. 1897.

Seventeen occurrence points studied. This would seem sufficient for reliable modelling, but the observed records are very scattered and do not fill the areas with the highest suitability. Most records occur in *Acacia-Commiphora* bushland proper, but some records have transgressed into transitional semi-evergreen bushland (Fig. 30).

No records have been observed from the areas with high or highest suitability in northern Ethiopia.

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* woodland, wooded grassland and bushland, often on red sandy soil overlying limestone but also on black cotton soil and on rocky slopes (Vollesen 1989). In Tropical East Africa (Kenya), it has been found growing in *Acacia-Commiphora* open bushland on eluvial soil (Gillett 1991). In Somalia, it has been known from both northern, central and southern parts of the country, growing in *Acacia-Commiphora* bushland (Thulin 1999).

Restricted to Ethiopia, Somalia, and northeastern Kenya. Not red-listed by IUCN.

C23. ***Commiphora ciliata*** Vollesen, Kew Bull. 40: 50. 1985.

Seven occurrence points studied. This is not sufficient for reliable modelling; the observed records are scattered and far from fill the areas with the highest suitability. Most of the few records occur in *Acacia-Commiphora* bushland proper, but one has been collected in transitional semi-evergreen bushland (Fig. 31).

No records have been observed from the areas with highest suitability in northern Ethiopia.

In Ethiopia, the species has been reported to grow in *Commiphora*, *Acacia-Commiphora* and *Acacia-Commiphora-Delonix* woodland and bushland on rocky limestone slopes (Vollesen 1989). In Tropical East Africa (Kenya), it has been found growing in *Acacia-Commiphora* bushland (Gillett 1991). In Somalia, it has been known from the central and southern parts, growing in *Acacia-Commiphora* bushland (Thulin 1999). In Ethiopia, Somalia, and northeastern Kenya. The extinction risk of the species is considered Near Threatened C1 by Alemu S, Alemu S, Atnafu H, Awas T, Belay B,

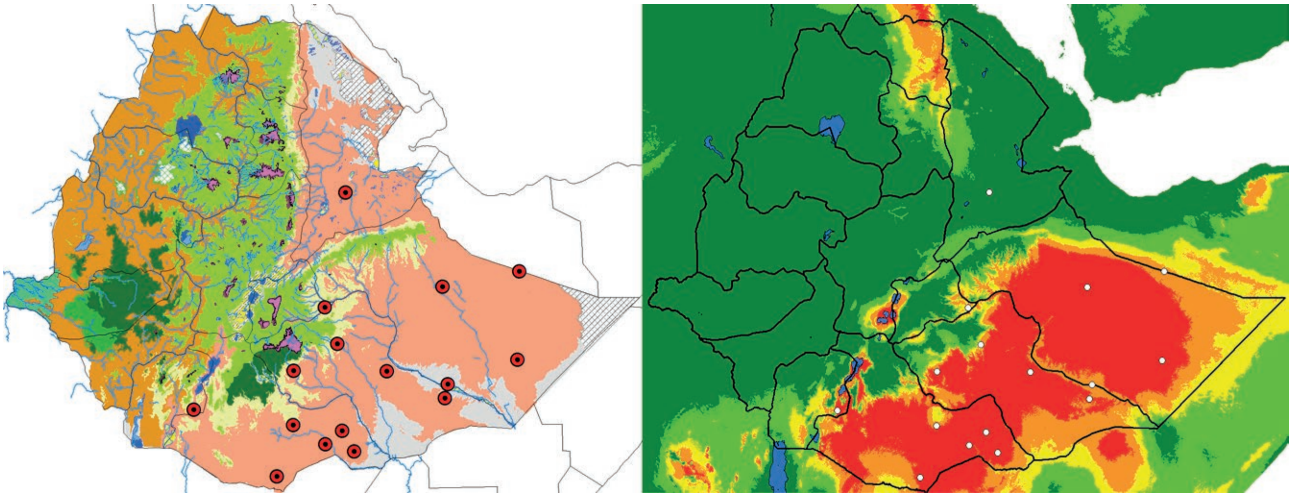


Figure 30. *Commiphora rostrata* Engl. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. One northern record is outside the predicted area. For text about species, see C22.

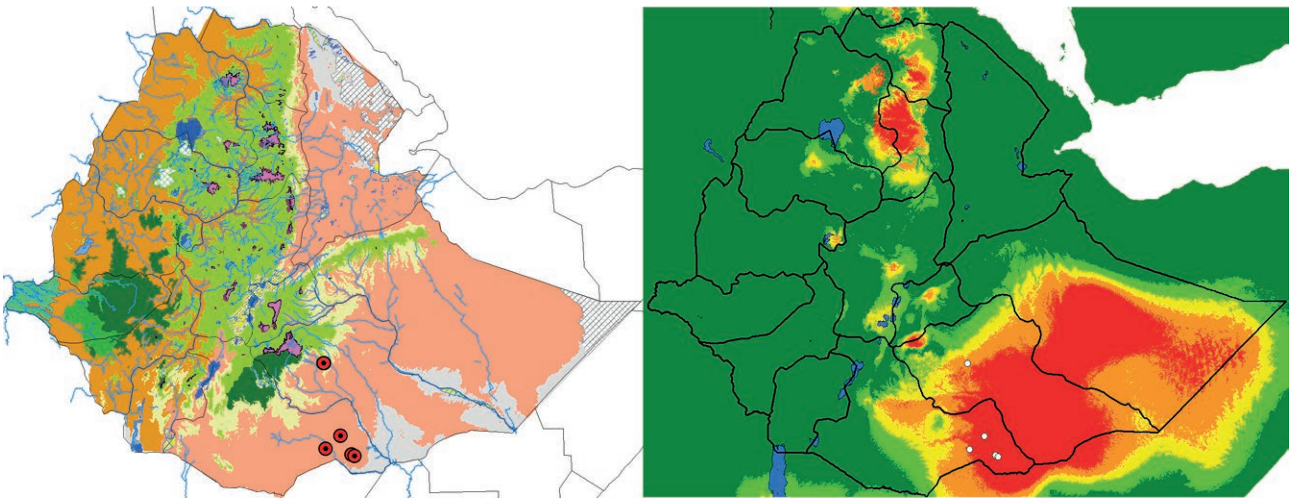


Figure 31. *Commiphora ciliata* Vollesen in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C23.

Demissew S, Luke WRQ, Mekbib E, Nemomissa S. 2021. *Commiphora ciliata* (errata version published in 2022). The IUCN Red List of Threatened Species 2021: e.T34440A223073030. https://doi.org/10.2305/IUCN.UK.2021-3.RLTS.T34440A223073030.en. The population size is declining, there is a continuing decline in area, extent and/or quality of habitat, and logging & wood harvesting.

C24. ***Commiphora erosa*** Vollesen, Kew Bull. 40: 60. 1985.

Four occurrence points studied. This is not sufficient for reliable modelling; the observed records have all been collected in semi-desert scrubland along the lower reaches of the Genale River (Fig. 32).

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* bushland on yellowish limestone alluvium and on gypsum hills (Vollesen 1989). In Tropical East Africa (Kenya), it has been found growing in open *Acacia-Commiphora* bushland usually on silty alluvium near perennial rivers (Gillett 1991). In Somalia, it has been known from the central and southern parts, growing in *Acacia-Commiphora* bushland, usually on silty soil (Thulin 1999).

In Ethiopia, Somalia, northeastern Kenya. Not redlisted by IUCN.

C25. ***Commiphora sphaerocarpa*** Chiov., Res. Sci. Somalia Ital. 1: 48. 1916.

Seven occurrence points studied. This is not sufficient for reliable modelling; the observed records are very scattered and far from filling the areas with the highest suitability. A few records occur in *Acacia-Commiphora* bushland proper, but most have been collected in semi-desert scrubland at the Genale and Webe Shebele rivers (Fig. 33).

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora-Boswellia rivae* bushland on rocky limestone and gypsum slopes (Vollesen 1989). In Tropical East Africa (Kenya), it was not yet found when the flora was published but it had been collected from near the Kenya-Somali border (Gillett 1991). In Somalia, the species is known from both the northern, central and southern parts, growing in *Acacia-Commiphora* bushland on limestone or gypsum, often in silty depressions, rarely on sand (Thulin 1999).

Restricted to Ethiopia and Somalia. The extinction risk of the species is considered Least Concern by Alemu S, Alemu S, Atnafu H, Awas T, Belay B, Demissew S, Luke WRQ, Mekbib E, Nemomissa S, Bahdon J. 2021. *Commiphora sphaerocarpa* (errata version published in 2022). The IUCN Red List of Threatened Species 2021: e.T128045093A223075447. https://doi.org/10.2305/IUCN.UK.2021-3.RLTS.T128045093A223075447.en. The trend of the population size is unknown, and nothing is known about decline in area, extent and/or quality of habitat.

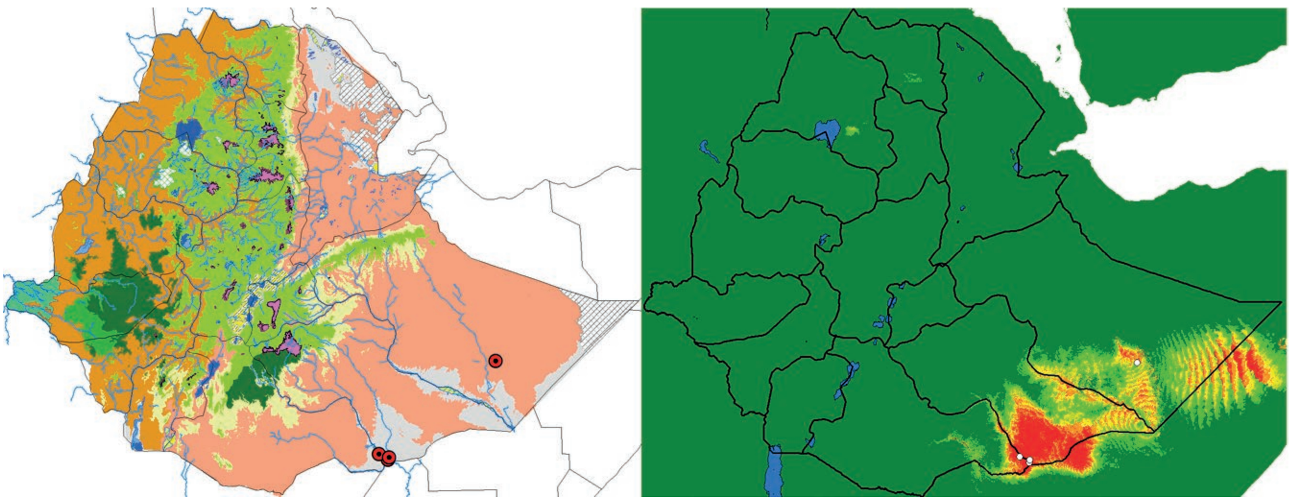


Figure 32. *Commiphora erosa* Vollesen in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C24.

C26. ***Commiphora mildbraedii*** Engl., Bot. Jahrb. Syst. 44: 145. 1910.

Four occurrence points in two nearly identical locations studied. This is not sufficient for reliable modelling; the observed records are scattered and far from filling areas with the highest suitability. Two records occur at the border between transitional semi-evergreen bushland and *Acacia-Commiphora* bushland proper, and two have been collected in semi-desert scrubland at the Webe Shebele River (Fig. 34).

In Ethiopia, the species has been reported to grow in dense *Acacia-Commiphora* bushland on black cotton soil or rocky limestone slopes (Vollesen 1989). In Tropical East Africa (Kenya, Tanzania), it has been found growing in *Acacia-Commiphora* bushland, especially in rocky places (Gillett 1991).

The species is widespread in Ethiopia, eastern Kenya, Tanzania. The extinction risk of the species is considered Least Concern by Luke WRQ, Musili P, Barasa J, Kalema J, Mathenge J, Nemomissa S, Bahdon J. 2021. *Commiphora mildbraedii* (errata version published in

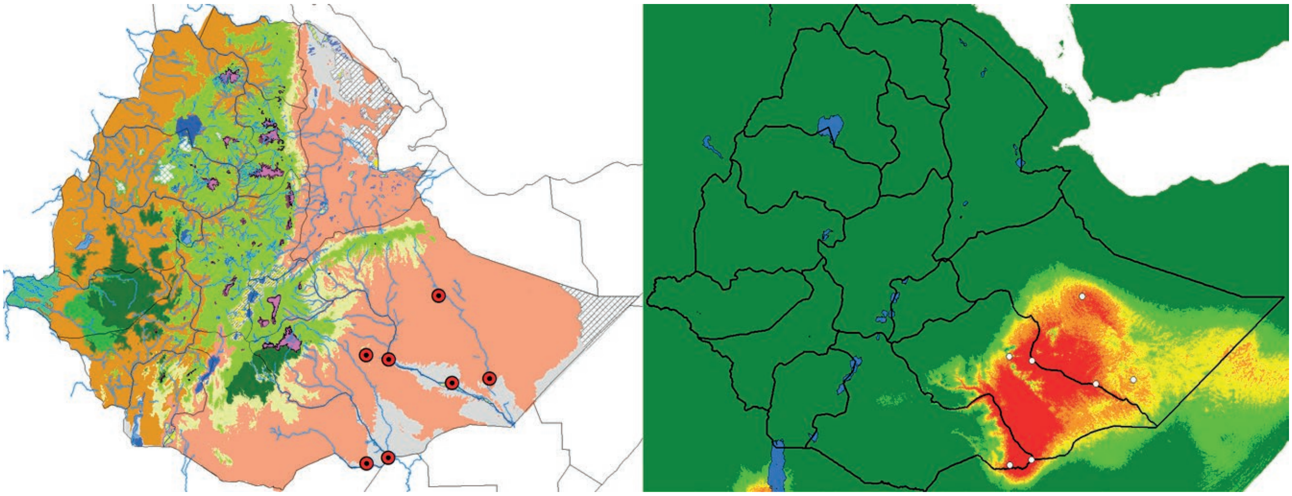


Figure 33. *Commiphora sphaerocarpa* Chiov. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C25.

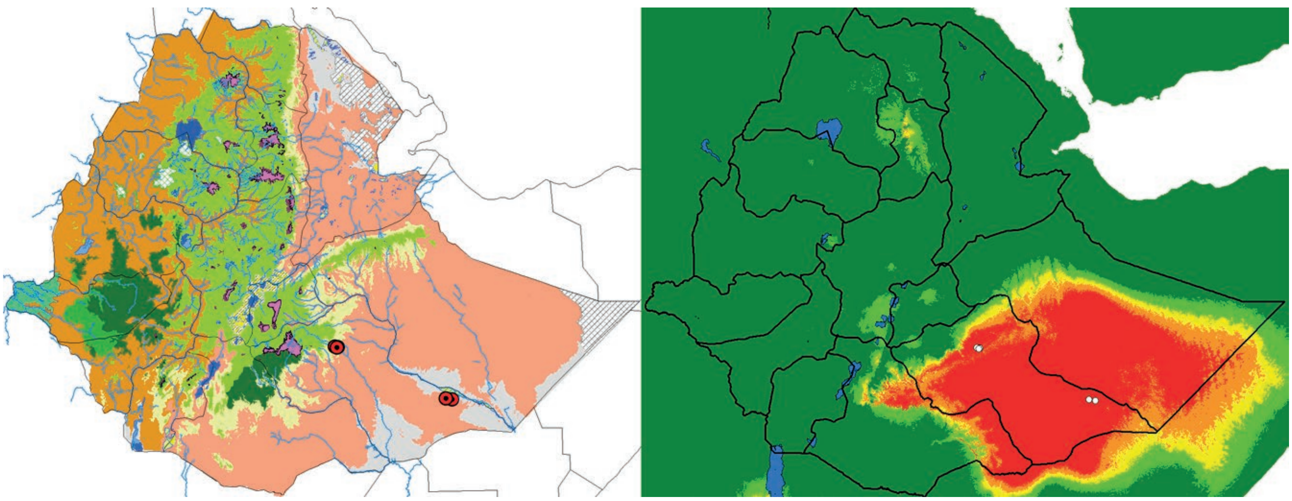


Figure 34. *Commiphora mildbraedii* Engl. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C26.

2022). The IUCN Red List of Threatened Species 2021: e.T128048477A223077813. https://doi.org/10.2305/IUCN.UK.2021-3.RLTS.T128048477A223077813.en. The trend in population size is decreasing.

C27. ***Commiphora cyclophylla*** Chiov., Fl. Somala 2: 88. 1932.

(=) *C. lughensis* Chiov., Fl. Somala 2: 105. 1932.

(=) *C. sp.* [= *Gilbert et al. 8170*].

Ten occurrence points from eight locations studied. This is not sufficient for reliable modelling; the observed records are scattered and far from filling the huge areas with highest suitability. Two records occur in the west near the Omo River on the border between semi-desert scrubland and *Acacia-Commiphora* bushland proper, three occurrence points occur in the south in *Acacia-Commiphora* bushland proper, and one occurs in the north in transitional semi-evergreen bushland (Fig. 35).

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* woodland and bushland on limestone slopes and ridges (this includes information about the material referred to *Commiphora* sp. [= *Gilbert et al. 8170*] (Vollesen 1989)). In Tropical East Africa (Kenya), it has been found growing in *Acacia-Commiphora* bushland on limestone (Gillett 1991). In Somalia, the species is known from the central and southern parts, growing usually on limestone or on gypsaceous ground (Thulin 1999).

Restricted to Ethiopia, Somalia, and northeastern Kenya. The extinction risk of the species is considered Vulnerable B2ab(iii) by Harvey-Brown Y. 2022. *Commiphora cyclophylla*. The IUCN Red List of Threatened Species 2022: e.T183101579A183101581. https://doi.org/10.2305/IUCN.UK.2022-2.RLTS.T183101579A183101581.en. The trend in the population size is unknown, there is a continuing decline in area, extent and/or quality of habitat, and the species is subject to Logging and wood harvesting.

C28. ***Commiphora campestris*** Engl., Bot. Jahrb. Syst. 15: 97. 1893.

Three occurrence points (from two locations) studied. This is not sufficient for reliable modelling; the records are all collected in *Acacia-Commiphora* bushland proper, and they are far from filling the large areas with the highest suitability (Fig. 36).

No records have been observed from the areas with highest suitability in northern Ethiopia.

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* bushland on rocky lava hills (Vollesen 1989). In Tropical East Africa (Kenya, Tanzania), it has been found growing in *Acacia-Commiphora* bushland and is widespread and very variable (Gillett 1991). In Somalia, the species is known from the central and southern parts, growing in deciduous bushland (Thulin 1999).

In Ethiopia, where it is rare, in eastern Kenya, and northeastern Tanzania, where it is widespread. The

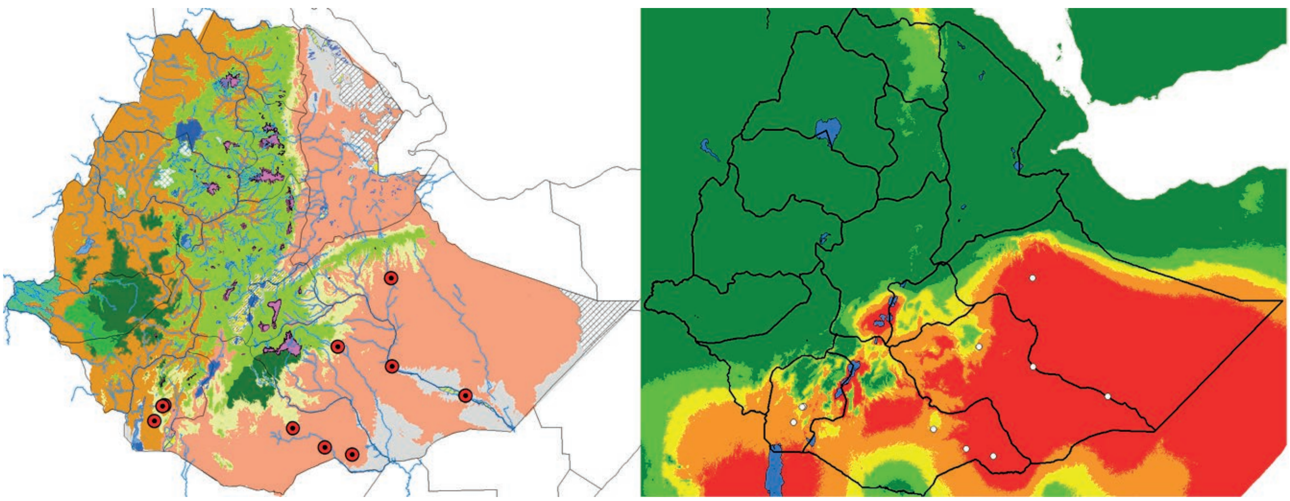


Figure 35. *Commiphora cyclophylla* Chiov. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C27.

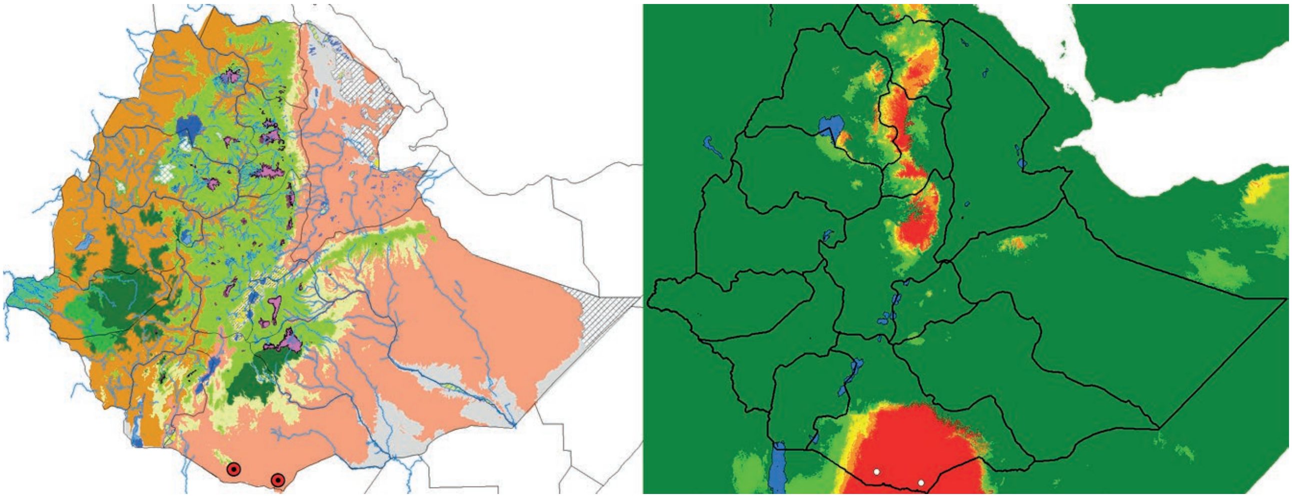


Figure 36. *Commiphora campestris* Engl. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C28.

extinction risk of the species is considered Least Concern by Beentje HJ, Gereau RE, Hilton-Taylor C, Howard G, Kindeketa W, Luke WRQ, Maunder M, Mwachala G, Mwangoka M, Ndangalasi H, Njau E-F, Schatz GE, Siro Masinde P, Wilkins VL. 2020. *Commiphora campestris*. The IUCN Red List of Threatened Species 2020: e.T62959A3117144. https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T62959A3117144.en. The trend in population size is unknown.

C29. ***Commiphora serrulata*** Engl., Bot. Jahrb. Syst. 15: 96. 1892.

Thirty-two occurrence points studied, which we consider sufficient for reliable modelling. The records studied are scattered within the areas with highest suitability, with the highest density in the wetter parts of *Acacia-Commiphora* bushland proper or transgressing into the transitional semi-evergreen bushland. One record has been made at the semi-desert scrubland along the Webe Shebele River (Fig. 37).

No record has been observed from the areas with highest suitability in northern Ethiopia.

The modelled omission rates of *C. serrulata* agree with the expected values, suggesting that the model performs as intended. The highest contribution to the model is provided by Bio4 (temperature seasonality).

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* woodland and bushland on limestone slopes and slopes of basaltic rocks, on level sandy soil and on black cotton soil (Vollesen 1989). In Somalia, the species is known from the northern parts, growing in semi-evergreen bushland (Thulin 1999).

Restricted to Ethiopia and Somalia. Not red-listed by IUCN.

C30. ***Commiphora gurreh*** Engl., Ann. Bot. (Rome) 7: 17 (1897).

(=) *C. tenuis* Vollesen, Kew Bull. 40: 48. 1985.

Seventeen occurrence points studied. This is sufficient for reliable modelling; the observed records are widely scattered and far from filling the huge areas with highest suitability. Some records occur on the border between transitional semi-evergreen bushland and *Acacia-Commiphora* bushland proper, others in *Acacia-Commiphora* bushland proper, one record was made in *Acacia* wooded grassland of the Rift Valley, and one record was made on the border between semi-desert scrubland and *Acacia-Commiphora* bushland proper (Fig. 38).

No record has been observed from the areas with highest suitability in northern Ethiopia.

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* woodland and bushland on rocky limestone slopes or black cotton soil (Vollesen 1989). In Tropical East Africa (Kenya), it has been found growing in *Acacia-Commiphora* bushland on various soils (Gillett 1991). In Somalia, the species is widespread in most of the country, where it has been found growing in *Acacia-Commiphora* bushland (Thulin 1999).

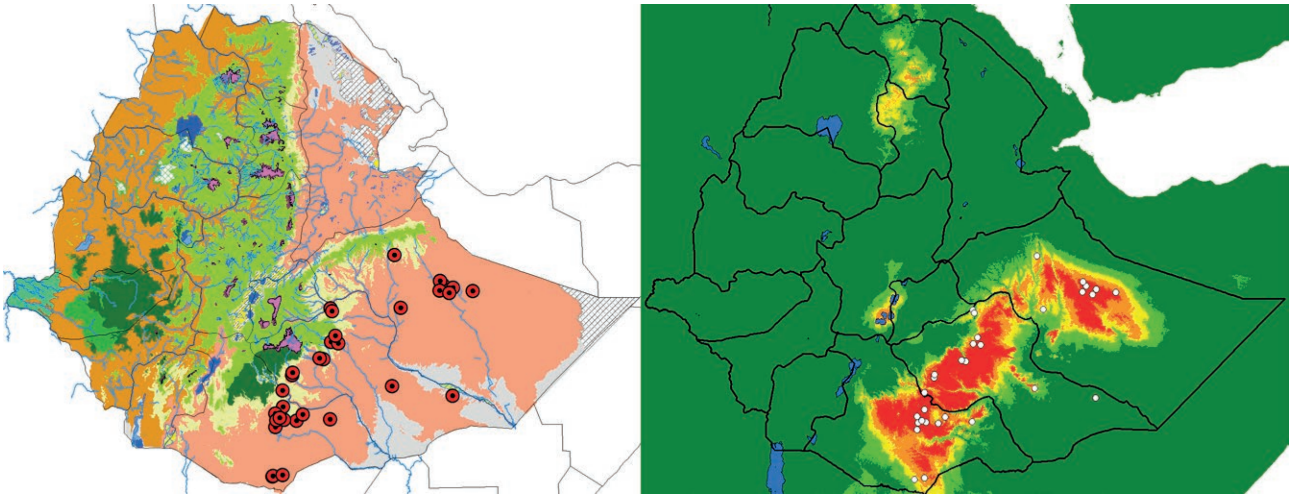


Figure 37. *Commiphora serrulata* Engl. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. One southeastern record is outside the predicted area. For text about species, see C29.

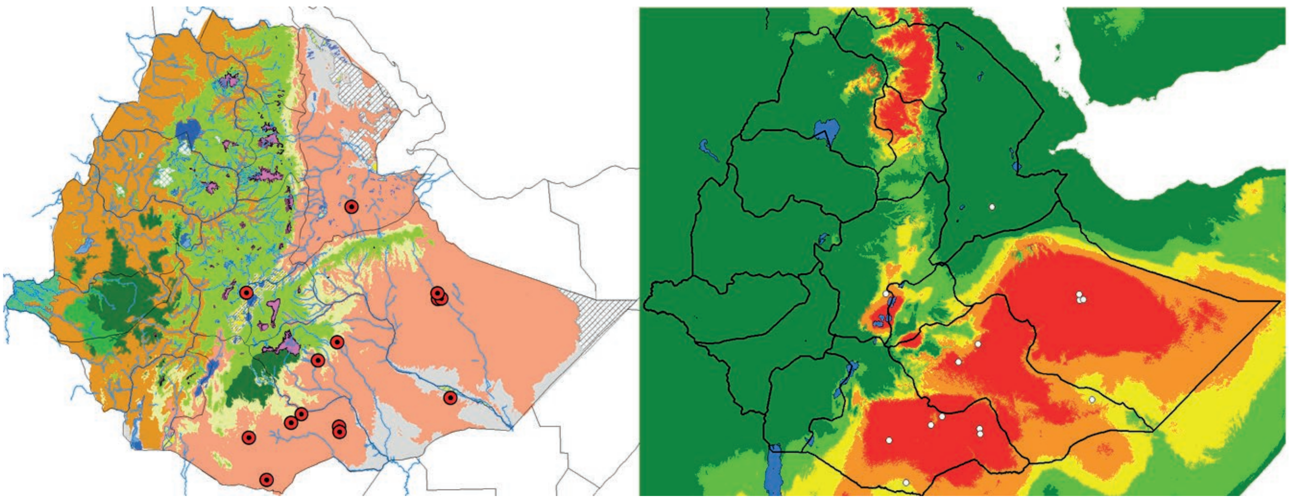


Figure 38. *Commiphora gurreh* Engl. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. One northern record is outside the predicted area. For text about species, see C30.

Restricted to Ethiopia, Somalia and northeastern Kenya. Not red-listed by IUCN.

C31. ***Commiphora quadricincta*** Schweinf., Bull. Herb. Boissier 7 (App. 2): 283. 1899.

Two occurrence points studied. This is absolutely not sufficient for reliable modelling; the only two observed records are widely scattered and far from filling the huge areas with the highest suitability in the Afar region, southeastern Ethiopia, and Somalia. One record is from *Acacia-Commiphora* bushland proper; another is from true desert (Fig. 39).

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* bushland, *Acacia-Adansonia* wooded grassland [presumably only recorded from Eritrea] on sandy soil, rocky slopes, and lava hills (Vollesen 1989).

The species is widespread from northern Nigeria and Tchad to eastern Sudan (Darbyshire et al. 2025), Eritrea and Ethiopia; also in Arabia. Not red-listed by IUCN.

C32. ***Commiphora hodai*** Sprague in Hooker's Icon. Pl. 32: t. 3111. 1927.

Five occurrence points (from four locations) studied. This is not sufficient for reliable modelling; the observed records are widely scattered and far from filling the huge areas with the highest suitability. Two records have been made in *Acacia-Commiphora* bushland proper, and two in semi-desert scrubland along the lower reaches of the Webe Shebele River (Fig. 40).

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* bushland on red sandy soil overlying limestone (Vollesen 1989). In Somalia, the species is recorded from *Acacia-Commiphora* bushland (Thulin 1999).

Restricted to Ethiopia and Somalia. The extinction risk of the species is considered Near Threatened by Thulin M. 1998. *Commiphora hodai*. The IUCN Red List of Threatened Species 1998: e.T35824A9960359. https://doi.org/10.2305/IUCN.UK.1998.RLTS.T35824A9960359.en. The trend in the population size is unspecified and the decline in area, extent and/or quality of habitat is unknown.

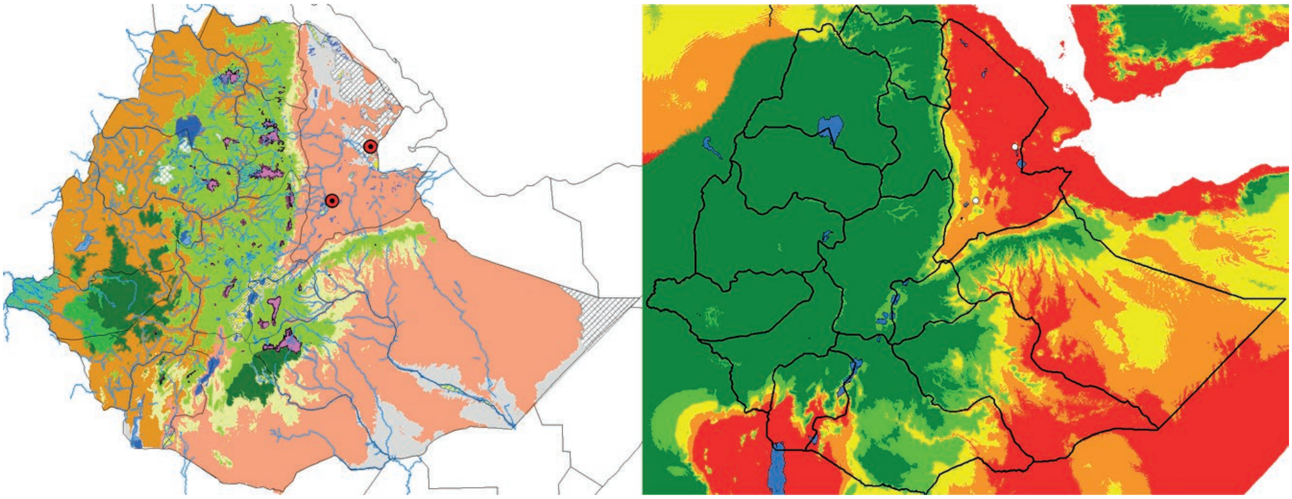


Figure 39. *Commiphora quadricincta* Schweinf. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. The predicted area is much larger than what the authors expect from field experience. For text about species, see C31.

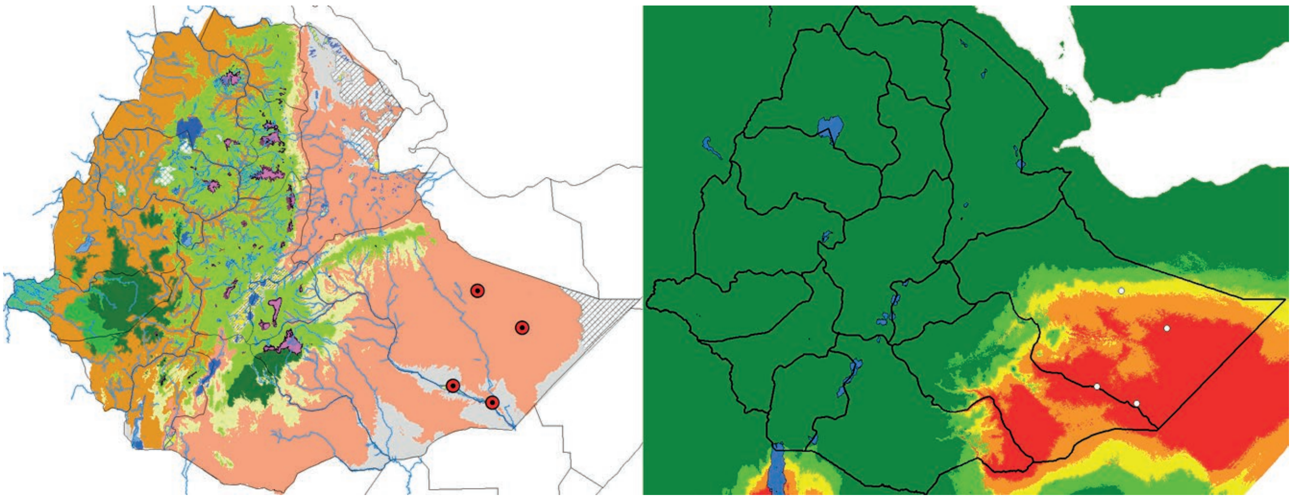


Figure 40. *Commiphora hodai* Sprague in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C32.

C33. ***Commiphora habessinica*** (O.Berg) Engl. in A.L.P.P. de Candolle & A.C.P. de Candolle, Monogr. Phan. 4: 10. 1883.

(=) *C. dancaliensis* Chiov., Ann. Bot. (Rome) 13: 403. 1915.

(=) *C. assaortensis* Chiov., Fl. Somala 2: 64. 1932.

(=) *C. bruceae* Chiov., Bull. Misc. Inform. Kew 1941: 133. 1941.

(=) *C. gracilispina* J.B.Gillett, Fl. Trop. E. Africa, Burserac.: 18. 1991.

Forty-nine occurrence points studied, which we consider sufficient for reliable modelling. The records studied are densely distributed in the areas with highest suitability in southern Ethiopia, where it occurs in *Combretum-Terminalia* woodland in the west, in *Acacia-Commiphora* bushland proper and in transitional semi-evergreen bushland in the middle, and in *Acacia-Commiphora* bushland proper, in transitional semi-evergreen bushland, and in semi-desert scrubland along the lower reaches of the Genale and Webe Shebele rivers. The species has also been recorded with one occurrence from *Combretum-Terminalia* woodland on the western escarpment of the Ethiopian highlands in Gambela (Illubabor) region, from *Combretum-Terminalia* woodland in the deep Didessa valley in the highlands (rivers running westwards to the Nile), and in transitional semi-evergreen bushland on the eastern escarpment of the Ethiopian highlands (Fig. 41).

The modelled omission rates of *C. habessinica* agree with the expected values, suggesting that the model performs as intended. The highest contribution to the model is provided by Bio3 (isothermality).

In Ethiopia, the species has been recorded to grow in *Acacia-Commiphora* bushland, sometimes with *Terminalia orbicularis*, in *Acacia-Balanites* woodland, *Anogeissus* woodland, on sandy to loamy soil overlying limestone and basement rock, on black cotton soil, and on lava hills; the tree is sometimes planted as hedges (Vollesen 1989). In Tropical East Africa (Uganda, Kenya, Tanzania), it has been found growing in *Acacia-Commiphora* open bushland on alluvium or red sandy loam (Gillett 1991). Thulin (1999) consider *C. habessinica* and *C. kua* as one variable species, and his habitat information is therefore not cited here. The species is widespread in Ethiopia, Eritrea, eastern Sudan, southwards to northern Mozambique and Zambia; also in Arabia. Not redlisted by IUCN.

C34. ***Commiphora sp.*** [= *Corradi 6767, 6768*].

One population studied, and hence the species is not modelled. The two gatherings are from the same population, or highly likely, from the same tree; the vegetation in the area is mixed but should probably be classified as *Acacia-Commiphora* bushland proper, near saline areas around Lake Chew Bahir (Fig. 42).

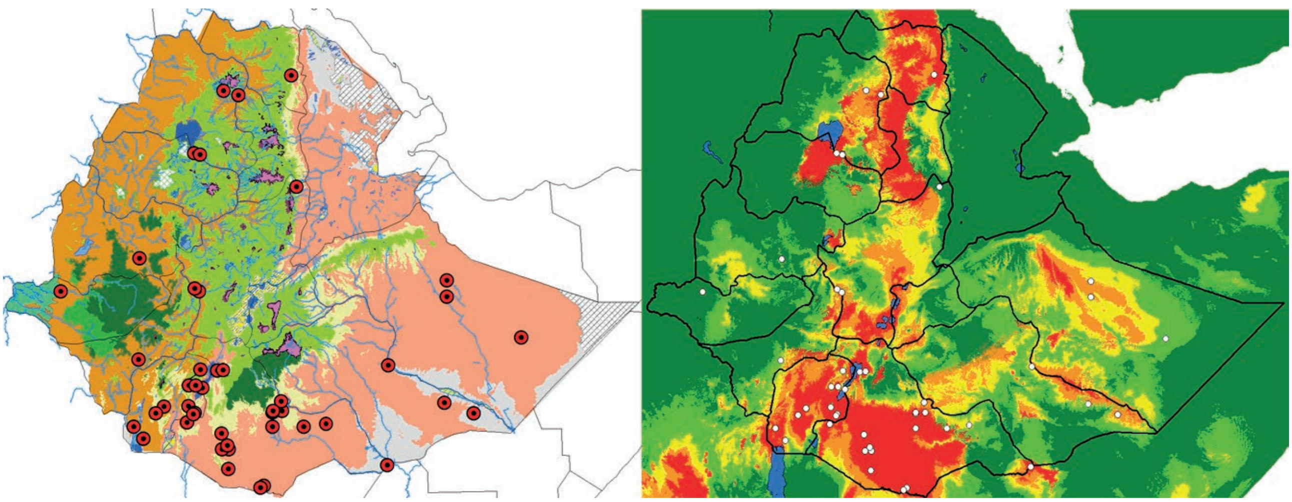


Figure 41. *Commiphora habessinica* (Berg) Engl. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. The western records (in WG and IL) are from narrow river valleys in the western moderate highlands of Ethiopia and can be expected to have climatic conditions different from the surrounding terrain. For text about species, see C33.

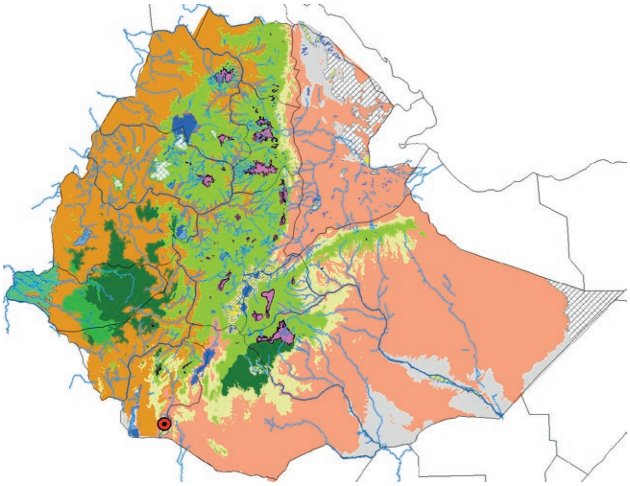


Figure 42. *Commiphora* sp. [= *Corradi 6767, 6768*]. Map showing distribution of observed records on the vegetation types in Fig. 1B. Modelling is not possible based on only one occurrence point. For text about species, see C34.

According to Vollesen (1989), it is known from *Acacia-Commiphora* bushland. Not known elsewhere. Not red-listed by IUCN.

C35. ***Commiphora kua*** (R.Br. ex Royle) Vollesen, Nordic J. Bot. 4: 37 (1984, published 1985).

(=) C. *flaviflora* Engl., Bot. Jahrb. Syst. 34: 304. 1904.

(=) *C. ellenbeckii* Engl., Bot. Jahrb. Syst. 34: 303. 1904.

(=) *C. crenulata* (A.Terrac.) Chiov., Ann. Bot. (Rome) 13: 404. 1915.

(=) *C. incisa* Chiov., Res. Sci. Somalia Ital. 1: 45. 1916.

(=) *C. candidula* Sprague in Hooker's Icon. Pl. 32: t. 3106. 1927.

(=) *C. gowlello* Sprague in Hooker's Icon. Pl. 32: t. 3109. 1927.

Seventy-three occurrence points studied, which we consider sufficient for reliable modelling. The records studied are densely distributed in areas with the highest suitability in southern Ethiopia, where it occurs in *Combretum-Terminalia* woodland in the west, in *Acacia-Commiphora* bushland proper and in transitional semi-evergreen bushland in the middle, and in *Acacia-Commiphora* bushland proper and in transitional semi-evergreen bushland and in semi-desert scrubland to the west of Genale River and along the lower reaches the Webe Shebele River. 3Two records have been made from *Acacia-Commiphora* bushland proper in the southern Afar region (Fig. 43).

The species has also been recorded from *Combretum-Terminalia* woodland in the deep valleys in the northern highlands (Tacazze river and tributaries running westwards to the Nile). The modelled omission rates of *C. kua* agree with the expected values, suggesting that the model performs as intended. The highest contribution to the model is provided by Bio12 (annual precipitation).

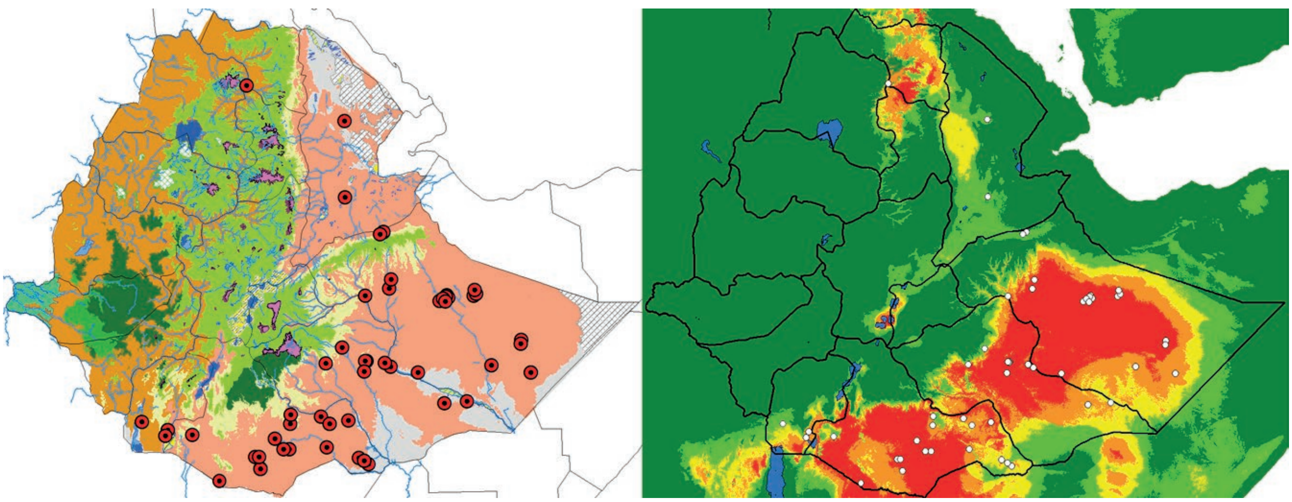


Figure 43. *Commiphora kua* (R. Br. ex Royle) Vollesen in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C35.

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* bushland, sometimes with *Terminalia orbicularis*, on yellowish, red to grey sandy or stony soil overlying limestone or basement rocks, on rocky slopes, or alluvial sandy loams in areas of poor drainage; this includes information on *C. ellenbeckii*, *C. incisa*, and *C. gowlello*, as recorded by Vollesen (1989). In Tropical East Africa (Kenya, Tanzania), it has been found growing in open *Acacia-Commiphora* bushland on rocky slopes and red sandy soil (Gillett 1991). Thulin (1999) consider *C. habessinica* and *C. kua* as one variable species, and his habitat information is therefore not cited here.

The species is widespread in Eritrea, Ethiopia, Somalia, northeastern and eastern Kenya; also in Arabia. Not red-listed by IUCN.

C36. ***Commiphora oddurensis*** Chiov., Fl. Somala 2: 71. 1932.

(=) *C. sp.* [= *Friis et al. 3160*].

(=) *C. oddurensis* Chiov. subsp. *suffruticosa* (Teshome) Sebsebe and Friis, Webbia 68: 143. 2013.

Seven occurrence points studied from five locations. This is not sufficient for reliable modelling; the observed records are very far from filling the huge areas with the highest suitability, and the locations fall into two groups, one in transitional semi-evergreen bushland and in *Acacia-Commiphora* bushland proper between Negele and Filtu, which is south of a tributary of the Genale River, and another in semi-desert scrubland along the lower reaches of the Webe Shebele River and one of its tributaries (Fig. 44).

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* bushland on rocky limestone ridges (Vollesen 1989), in *Acacia-Commiphora* woodland, bushland or open bushland, on rocky limestone slopes, in stony soil over rocks, or on brown, orange and red sand and brown soil. As a whole, the species seems to be associated with limestone or gypsum (Demissew and Friis 2013). In Tropical East Africa (Kenya), it has been found growing in *Acacia-Commiphora* bushland on limestone slopes (Gillett 1991). In Somalia, it grows in *Acacia-Commiphora* bushland on sand or limestone (Thulin 1999).

Restricted to Ethiopia, Somalia, and northeastern Kenya. The extinction risk of the species is considered Least Concern by Kalema J, Musili P, Barasa J, Nemomissa S, Bahdon J. 2021. *Commiphora oddurensis* (errata version published in 2022). The IUCN Red List of Threatened Species 2021: e.T128048544A223077946. https://doi.org/10.2305/IUCN.UK.2021-3.RLTS.T128048544A223077946.en.

Demissew and Friis (2013) also assessed Least Concern for both subspecies and the species as a whole.

Syn.: *C. suffruticosa* Teshome (2006); *C. oddurensis* subsp. *suffruticosa* (Teshome) Sebsebe & Friis (2013).

The author designation "Teshome" in IPNI, etc., refers to Teshome Soromessa, here in the list of references as "Soromessa T." The trend in population size is unknown. There is a continuing decline in the number of mature individuals.

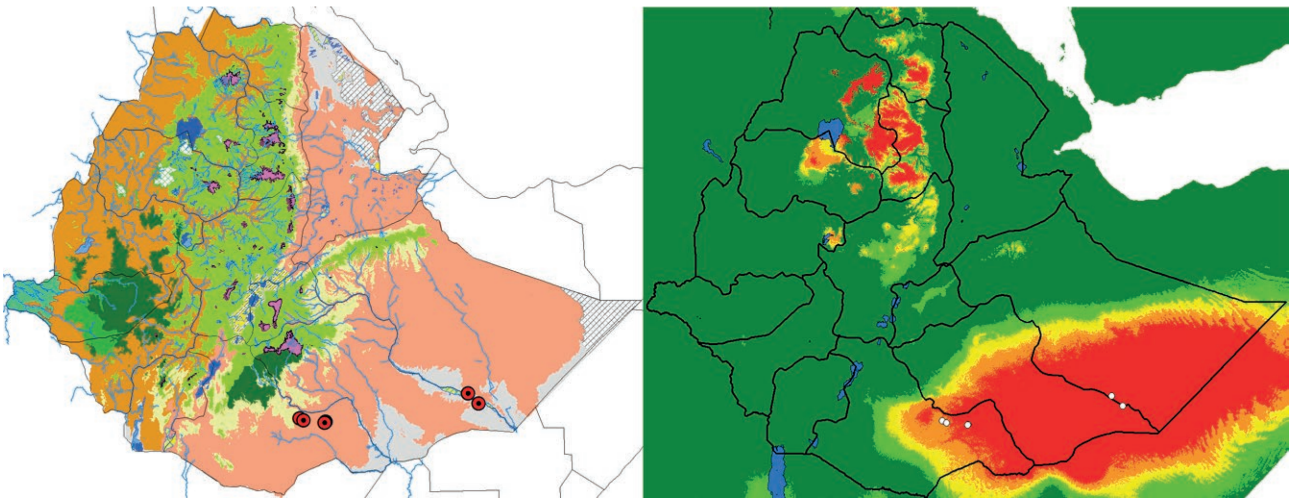


Figure 44. *Commiphora oddurensis* Chiov. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C36.

C37. ***Commiphora horrida*** Chiov., Fl. Somala 2: 87. 1932.

Four occurrence points studied. This is not sufficient for reliable modelling; the observed records are far from filling the huge areas with highest suitability. The collections have been made from the driest parts of eastern Ethiopia, from the border between *Acacia-Commiphora* bushland proper and semi-desert scrubland or desert (Fig. 45).

In Ethiopia, the species has been reported to grow in dry open *Acacia-Commiphora* bushland on fine, sometimes shifting, sandy soil overlying limestone (Vollesen 1989). In Somalia, the species occurs in the central and southern parts, growing on sand, sand over limestone, or on gypsum (Thulin 1999).

Restricted to Ethiopia and Somalia. Not red-listed by IUCN.

C38. ***Commiphora boranensis*** Vollesen, Kew Bull. 40: 64. 1985.

(=) *C. sp.* [= *Gilbert et al. 8171*].

Fifteen occurrence points studied. This just sufficient for reliable modelling, but the observed records can hardly fill the huge areas with highest suitability, falling in three groups, one in *Combretum-Terminalia* woodland near the Omo River, one in southern Ethiopia in areas with a mosaic of transitional semi-evergreen bushland and *Acacia-Commiphora* bushland proper, and a third group in the drier parts of *Acacia-Commiphora* bushland in eastern Ethiopia (Fig. 46).

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* woodland and bushland on rocky limestone slopes and black cotton soil, and on gypsum hills (Vollesen 1989). In Tropical East Africa (Kenya), it has been found growing in *Acacia-Commiphora* bushland (Gillett 1991).

Restricted to Ethiopia and northeastern Kenya. The extinction risk of the species is considered Least Concern by Alemu S, Alemu S, Atnafu H, Awas T, Belay B, Demissew S, Luke WRQ, Musili P, Nemomissa S. 2021. *Commiphora boranensis* (errata version published in 2022). The IUCN Red List of Threatened Species 2021: e.T128044306A223075076. https://doi.org/10.2305/IUCN.UK.2021-3.RLTS.T128044306A223075076.en. The trend in population size is unknown.

C39. ***Commiphora sp.*** [= *Gilbert et al. 7652*].

One occurrence point studied, and hence the species is not modelled. The collection was made from *Acacia-Commiphora* bushland proper, but near semi-desert scrubland along the Genale River (Fig. 47).

In Ethiopia, it has been reported to grow in *Acacia-Commiphora* bushland on stony limestone ridges (Vollesen 1989). Not known elsewhere. Not red-listed by IUCN.

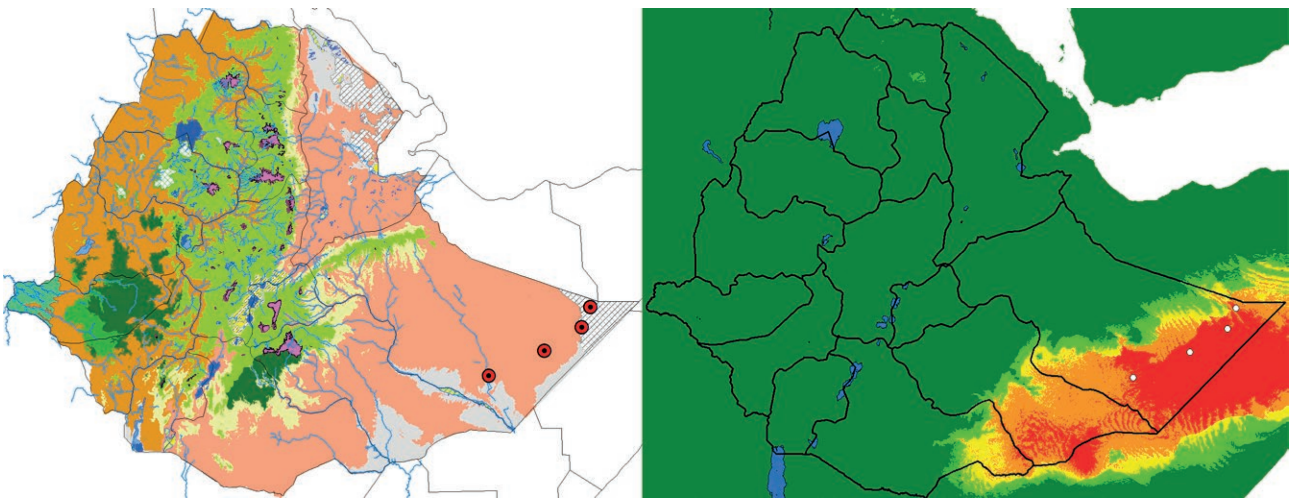


Figure 45. *Commiphora horrida* Chiov. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C37.

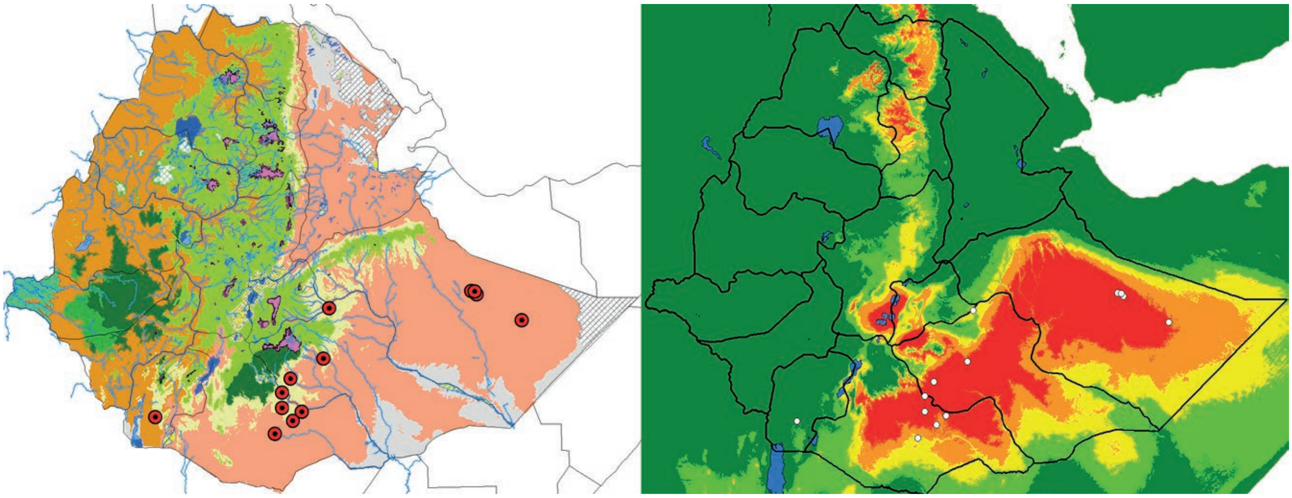


Figure 46. *Commiphora boranensis* Vollesen in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C38.

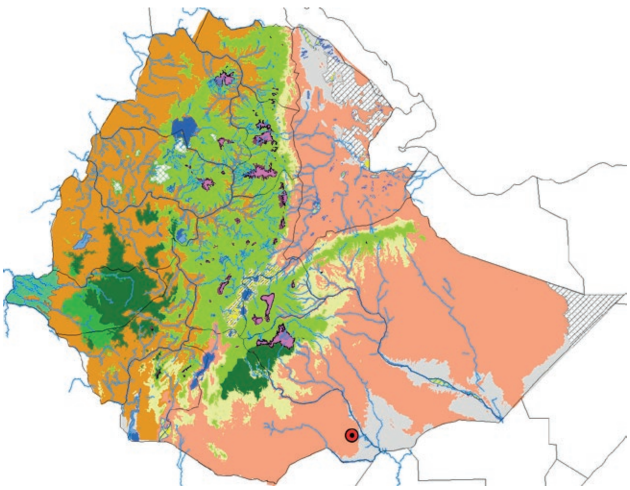


Figure 47. *Commiphora* sp. [= *Gilbert et al. 7652*] Map showing distribution of observed records on the vegetation types in Fig. 1B. Modelling is not possible on only one occurrence point. For text about species, see C39.

C40. ***Commiphora gileadensis*** (L.) C.Chr., Dansk. Bot. Ark. 4(3): 18. 1922.

(=) *C. albiflora* Engl., Bot. Jahrb. Syst. 34: 310. 1904.

(=) *C. velutina* Chiov., Res. Sci. Somalia Ital. 1: 47. 1916.

(=) *C. ancistrophora* Chiov., Fl. Somala 2: 111. 1932.

(=) *C. coronillifolia* Chiov., Fl. Somala 2: 101. 1932.

Nineteen occurrence points studied, which we consider sufficient for reliable modelling. The records studied are scattered in southern and eastern Ethiopia, including the southern part of Afar region, where one northernmost record is outside the predicted area. Collections have been made from *Acacia-Commiphora* bushland proper, but some are from near semi-desert scrubland close to the lower reaches of the Genale and Webe Shebele rivers (Fig. 48).

The modelled omission rates of *C. gileadensis* agree with the expected values, suggesting that the model may perform as intended. The highest contribution to the model is provided by Bio4 (temperature seasonality).

In Ethiopia, the species has been reported to grow in *Acacia-Commiphora* bushland on red to grey sandy soil overlying limestone and basement rocks, on rocky limestone ridges, in semi-desert bushland, often on rocky hills, and on old lava flows (Vollesen 1989). In Tropical East Africa (Kenya), it has been found growing in *Acacia-Commiphora* bushland on limestone hills (Gillett 1991). In Somalia, it grows in *Acacia-Commiphora* bushland and semi-desert scrub (Thulin 1999).

The species is widespread in eastern Sudan (Darbyshire et al. 2015), Eritrea, Ethiopia, Djibouti, Somalia, northeastern Kenya; also in Egypt and Arabia. Not redlisted by IUCN.

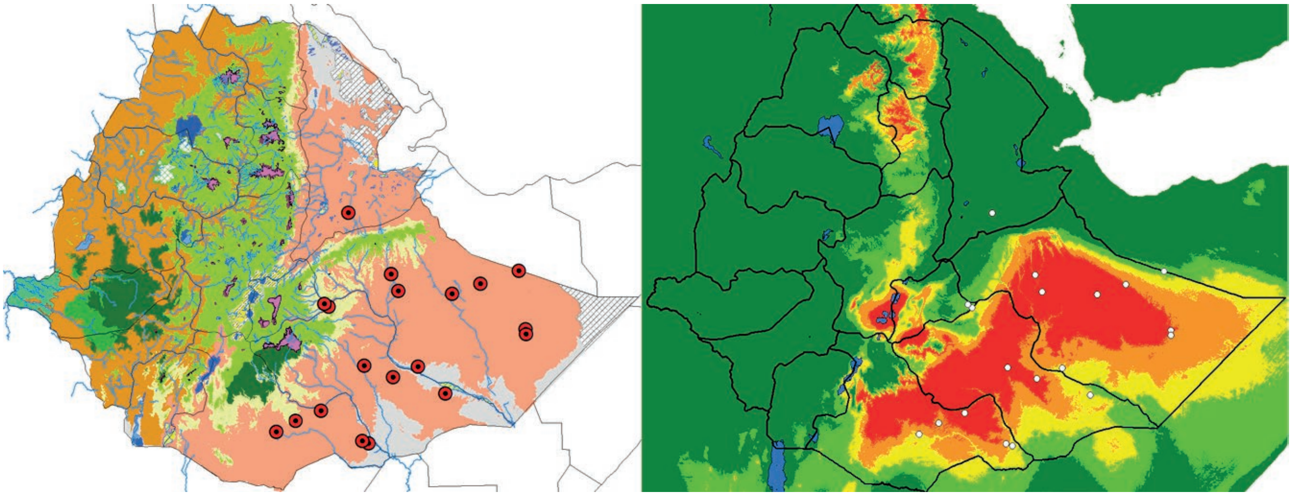


Figure 48. *Commiphora gileadensis* (L.) C. Chr. in Ethiopia. Left hand map showing distribution of observed records on the vegetation types in Fig. 1B; right hand map showing modelled suitability of potential distribution areas of the species as defined in Fig. 2, based on climatic parameters. For text about species, see C40.

C41. ***Commiphora chiovendana*** J.B.Gillett ex Thulin, Nordic J. Bot. 20: 405. 2000 [2001].

(=) *C. sp.* [= *Glover & Gilliland 973*].

One occurrence point studied, and hence the species is not modelled. The collection was made in semi-desert scrub (Fig. 49).

The species has been reported to grow in *Acacia-Commiphora* bushland on red sandy soil overlying limestone (Vollesen 1989). In Somalia, it has been reported from the northern and central parts, growing in *Acacia-Commiphora* bushland on red sandy or silty soil overlying limestone, occasionally gypseous (Thulin 1999).

Restricted to Ethiopia and Somalia. The extinction risk of the species is considered Least Concern by Jama F. 2024. *Commiphora chiovendana*. The IUCN Red List of Threatened Species 2024: e.T215410234A219277318. https://doi.org/10.2305/IUCN.UK.2024-2.RLTS.T215410234A219277318.en. The trend in the population size is unknown; the species is only marginally present in Ethiopia but occurs as fairly widespread in the northern and central regions of Somalia. The species has an estimated extent of occurrence (EOO) of 242,002 km^2 and an area of occupancy (AOO) of 120 km^2. There is concern due to a decline in area, extent and/or quality of habitat.

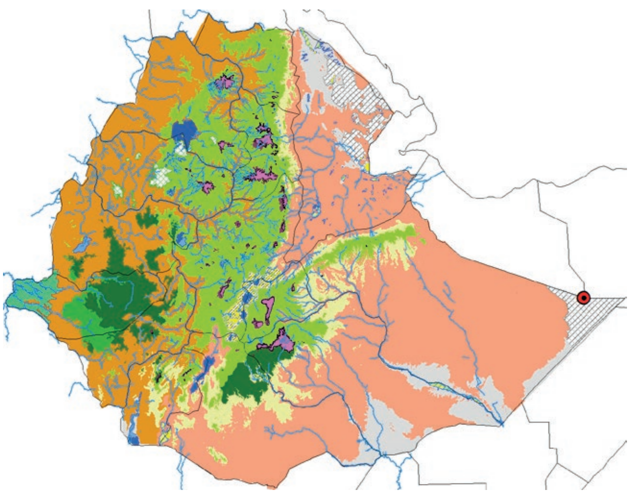


Figure 49. *Commiphora chiovendana* Gillett ex Thulin in Ethiopia. Map showing distribution of observed records on the vegetation types in Fig. 1B. Modelling is not possible based on only one occurrence point. For text about species, see C41.

C42. ***Commiphora multifoliolata*** Gillett ex Thulin, Nordic J. Bot. 20: 407. 2000 [in fact 2001].

One occurrence point studied, and hence the species is not modelled. The collection was made in semi-desert scrubland near the lower reach of the Webe Shebele River, and in saline wetlands along the river (Fig. 50).

In Somalia, it has been known from the southern parts adjacent to the Ethiopian record, growing in *Acacia-Commiphora* bushland on limestone (Thulin 1999).

Restricted to eastern Ethiopia and southern Somalia. Not red-listed by IUCN, but a conservation assessment made on all available material would be desirable.

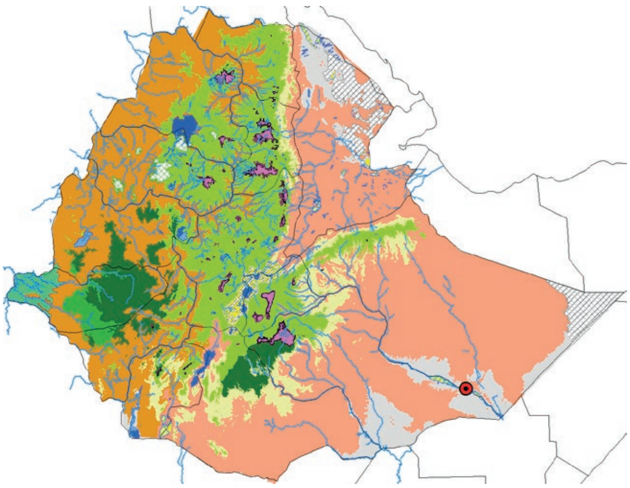


Figure 50. *Commiphora multifoliolata* Gillett ex Thulin in Ethiopia. Map showing distribution of observed records on the vegetation types in Fig. 1B. Modelling is not possible based on only one occurrence point. For text about species, see C42.

THE SPECIES OF BURSERACEAE IN ETHIOPIAN VEGETATION TYPES

The association of Ethiopian Burseraceae species with the vegetation types accepted by Friis et al. (2010, 2022) has been listed in Table 1, based on our interpretation of the left-hand maps in the Figs. 1–50. The recorded observations on the maps in this work are shown as red bird-eye dots. In Table 1, transgressing species are indicated in sharp brackets.

As documented in this account, both in our new observations in this work and in observations recorded in the Flora of Ethiopia [and Eritrea] (Vollesen 1989) in its precursor with taxonomic novelties (Vollesen 1985), Flora of Tropical East Africa (Gillett (1991), and Flora of Somalia (Thulin 1999), it is almost consistently stated that all the Ethiopian species of *Commiphora* occur in *Acacia-Commiphora* bushland and woodland (or, when the taxonomic splitting of *Acacia* is applied in the description of vegetation types, referred to as *Senegalia-Vachellia-Commiphora* woodland or bushland). Here, we confirm that the species are very often associated with limestone rocks, limestone with gypsum, and red or grey sand overlying limestone or gypsum. Occasionally, a few species of Burseraceae may also grow in *Acacia-Commiphora* bushland and woodland on sand over basement or granite rocks (*Boswellia neglecta*, *Commiphora edulis* subsp. *boiviniana*, *C. samharensis*, *C. schimperi*, *C. confusa*, *C. kataf*, *C. habessinica*, *C. kua*, and *C. gileadensis*).

Only *Commiphora staphyleifolia*, *C. unilobata*, and *C. erosa* have been reported to grow on alluvial soil, but again, these are probably derived from limestone or gypsum. A number of species that grow in *Acacia-Commiphora* bushland and woodland penetrate into transitional semi-evergreen bushland at their upper distributional limits (see Table 1).

Some widespread species (*Boswellia neglecta*, *Commiphora edulis* subsp. *boiviniana*, *C. samharensis*, *C. schimperi*, *C. africana*, *C. confusa*, *C. kataf*, *C. habessinica*, *C. kua*, and *C. boranensis*) grow in *Acacia-Commiphora* bushland and woodland, but frequently or often penetrate into *Combretum-Terminalia* woodland. Only *Boswellia papyrifera*, *B. pirottae*, and *Commiphora pedunculata* have their main distribution in *Combretum-Terminalia* woodland. A hardy group of species occur in semi-desert scrubland, desert, and in saline wetlands (see Table 1).

POTENTIAL DISTRIBUTIONS OF THE ETHIOPIAN BURSERACEAE BASED ON CLIMATIC PARAMETERS AND OBSERVED DISTRIBUTION

In Table 2 there is a survey based on our interpretation of the right-hand maps in the Figs. 3–9, 11–41, and 43–48. In these maps the observed distributions, shown as white dots, have been superimposed on the modelled suitability based on climatic parameters, as described in Materials and Methods.

Names of species that according to our estimate partly fill the area of highest predicted suitability on climatic parameters in some part of the predicted area, but not in the whole area, are indicated in sharp brackets. In Table 3 we have listed the species that according to climatic parameters are predicted to occur in northern Ethiopia. Among the species with high probability of occurring in northern Ethiopia, particularly along the eastern escarpment of the highlands, we have separately listed those that that have been and those that have not been recorded from there. We can offer no explanation for these patterns; some may erroneously have been predicted to occur in northern Ethiopia because of insufficient data, others may be restricted from northern Ethiopia due to unobserved environmental factors or for historical reasons.

The modelled patterns vary, particularly if the number of observed locations is lower than 12–13. For the following species we find a characteristic modelled pattern which is similar for a number of fairly widespread species listed here (Table 2): *Boswellia neglecta*, *B. microphylla*, *Commiphora myrrha*, *C. samharensis*, *C. hildebrandtii*, *C. corrugata*, *C. kataf*, *C. serrulata*, [*C. gurreh*], *C. kua*, *C. boranensis*, and *C. gileadensis*. The predicted pattern consists of a large area in HA and smaller, but

Table 1. Species that are recorded from the potential vegetation types proposed by Friis et al. (2010) and Friis et al. (2022) and recognized in this paper. Species marginally transgressing species into vegetation types without being widely distributed in these vegetation types are indicated in sharp brackets. B: *Boswellia*, C: *Commiphora*.

Potential vegetation type	Species in potential vegetation types and marginally transgressing into vegetation types without being widely distributed there [indicated in sharp brackets]. B. stands for *Boswellia*; C. for *Commiphora*	Number of species
Acacia wooded grassland of the Rift Valley	*C. schimperi*; [*C. gurreh*]	One species of *Commiphora* as widespread in the vegetation type; one species of *Commiphora* as marginal intruder
Acacia-Commiphora woodland and bushland proper	*B. papyrifera*; *B. rivae*; *B. neglecta*; *B. microphylla*; *B. neglecta*; *B. microphylla*; [*C. erlangeriana*]; [*C. paolii*]; *C. edulis* subsp. *boiviniana*; *C. sphaerophylla*; *C. myrrha*; *C. samharensis*; *C. schimperi*; *C. obovata*; *C. africana*; *C. hildebrandtii*; *C. ogadensis*; *C. corrugata*; *C. truncata*; *C. confusa*; *C. kataf*; *C. rostrata*; *C. ciliata*; [*C. sphaerocarpa*]; [*C. mildbraedii*]; *C. cyclophylla*; *C. campestris*; *C. serrulata*; *C. gurreh*; *C. quadricincta*; *C. hodai*; *C. habessinica*; *C. sp. = Corradi 6767, 6768*; *C.* kua; *C. oddurensis*; *C. horrida*; *C. boranensis*; *C. sp. = Gilbert et al. 7652*; *C. gileadensis*	Seven species of *Boswellia* and thirty-one species of *Commiphora* as widespread in the vegetation type; four species of *Commiphora* as marginal intruders
Combretum-Terminalia woodland and wooded grassland	*B. papyrifera*; *B. pirottae*; [*B. neglecta*]; *C. edulis* subsp. *boiviniana*; *C. schimperi*; *C. africana; C. pedunculata*; [*C. confusa*]; [*C. cyclophylla*]; *C. habessinica; C. kua*; *C. boranensis*	Two species of *Boswellia* and seven species of *Commiphora* as widespread in the vegetation type; one species of *Boswellia* and two species of *Commiphora* as marginal intruders
Desert	[*B. rivae*]; *B. ogadensis*; *C. quadricincta*; *C. horrida*; *C. chiovendana*	One species of *Boswellia*, and three species of *Commiphora* as widespread in the vegetation type; one species of *Boswellia* as marginal intruder
Saline wetland	[*B. rivae*]; *B. ogadensis*; [*B. microphylla*]	One species of *Commiphora* as widespread in the vegetation type; two species of *Commiphora* as marginal intruders
Semi-desert scrubland	[*B. rivae*]; *B. ogadensis*; [*B. microphylla*]; [*B. microphylla*]; *C. erlangeriana*; *C. staphyleifolia*; *C. unilobata*; *C. guidottii*; [*C. paolii*]; *C. myrrha;* [*C. samharensis*]; *C. africana*; [*C. truncata*]; [*C. confusa*]; *C. kataf*; *C. erosa*; *C. sphaerocarpa*; [*C. mildbraedii*]; [*C. serrulata*]; [*C. gurreh*]; *C. hodai*; *C. habessinica*; *C. kua*; *C. oddurensis*; [*C. sp. = Gilbert et al. 7652*]; [*C. gileadensis*]; *C. multifoliolata*	Fifteen species of *Commiphora* as widespread in the vegetation type; ten species of *Commiphora* as marginal intruders
Transitional semi-evergreen bushland	[*B. rivae*]; [*B. neglecta*]; [*B. microphylla*]; [*B. neglecta*]; [*B. microphylla*]; [*C. guidottii*]; [*C. edulis* subsp. *boiviniana*]; [*C. sphaerophylla*]; [*C. myrrha*]; [*C. samharensis*]; [*C. obovata]*; [*C. africana*]; *C. monoica*; *C. ogadensis*; [*C. corrugata*]; [*C. confusa*]; *C. alaticaulis*; [*C. kataf*]; [*C. rostrata*]; [*C. ciliata*]; [*C. mildbraedii*]; [*C. cyclophylla*]; [*C. serrulata*]; [*C. gurreh*]; *C. habessinica*; *C. kua*; [*C. oddurensis*]; [*C. boranensis*]	Four species of *Commiphora* as widespread in the vegetation type; five species of *Boswellia* and nineteen species of *Commiphora* as marginal intruders

usually coherent areas in BA and SD, reaching as far as or into GG. Just to describe the outline of this pattern, it might be tempting to compare it with the outline of a large quadruped waking on its hind legs, with small forelimbs and a large head. This may agree with a particular pattern of climatic parameters suitable for *Commiphora*. The predicted pattern of *C. gurreh* does not agree as well to this outline as the other species in the list. A similar pattern with less clearly defined outlines is suggested by the model for all species shown in Fig. 2.

We cannot satisfactorily suggest why the observed distribution of some species do not fill the modelled distribution based on climatic parameters. It can be due to insufficient collecting activity or due to lack of observed environmental factors that limit the distribution of the species, but have not been incorporated into our models.

Table 2. Species of Burseraceae filling, partially filling and far from filling their modelled area of distribution; species with a modelled distribution that forms a repeated pattern with a large area in HA and connected but more restricted areas in BA and SD, stretching to GG. B: *Boswellia*; C: *Commiphora*.

Species which approximately fill the area of highest suitability predicted on climatic parameters	*B. papyrifera*; *B. pirottae*; *B. rivae*; [*B. ogadensis*]; *B. neglecta*; *B. microphylla*; *C. edulis* subsp. *boiviniana*; [*C. africana*]; [*C. pedunculata*]; [*C. confusa]*; *C. serrulata*; *C. habessinica*	Five species of *Boswellia* approximately filling the area of highest suitability predicted on climatic parameters; one species of *Boswellia* filling the area of highest suitability predicted on climatic parameters well in part. Two species of *Commiphora* approximately filling the area of highest suitability predicted on climatic parameters; three species of *Commiphora* filling the area of highest suitability predicted on climatic parameters well in part.
Species which far from fill the area predicted on climatic parameters	*C. erlangeriana*; *C. unilobata*; *C. guidottii*; *C. paolii*; *C. sphaerophylla*; *C. myrrha*; *C. samharensis*; *C. schimperi*; *C. obovata*; *C. monoica*; *C. hildebrandtii*; *C. corrugata*; *C. truncata*; *C. alaticaulis*; *C. kataf*; *C. rostrata*; *C. ciliata*; *C. sphaerocarpa*; *C. mildbraedii*; *C. cyclophylla*; *C. campestris*; *C. gurreh*; *C. quadricincta*; *C. hodai*; *C. kua*; *C. oddurensis*; *C. horrida*; *C. boranensis*; *C. gileadensis*	Twenty-nine species of *Commiphora* far from filling the area predicted on climatic parameters.
Species with a modelled distribution that forms a characteristic repeated pattern in several species (with a large area in HA and connected but more restricted areas in BA and SD, stretching to GG; some of these species have predicted area in northern Ethiopia)	*B. neglecta*; *B. microphylla*; *C. myrrha*; *C. samharensis*; *C. hildebrandtii*; *C. corrugata*; *C. kataf*; *C. serrulata*; [*C. gurreh*]; *C. kua*; *C. boranensis*; *C. gileadensis*	Two species of *Boswellia* and ten species of *Commiphora* with similar and repeated predicted distribution patterns; one species of *Commiphora* not quite typical.

Table 3. Species of *Commiphora* with main distribution in southeastern distribution in Ethiopia but predicted also to occur in northern Ethiopia. The species that actually occur in northern Ethiopia and those that do not occur there are listed separately.

Species predicted on climatic parameters to occur in northern Ethiopia and do occur there	*C. schimperi*; *C. africana*; *C. habessinica*; *C. kua*	Four species of *Commiphora* predicted on climatic parameters to occur in northern Ethiopia and do occur there
Species predicted on climatic parameters to occur in northern Ethiopia but do not	*C. samharensis*; *C. obovata*; *C. monoica*; *C. pedunculata*; *C. hildebrandtii*; *C. ogadensis*; *C. corrugata*; *C. confusa*; *C. alaticaulis*; *C. kataf*; *C. rostrata*; *C. ciliata*; *C. campestris*; *C. serrulata*; *C. gurreh*; *C. oddurensis*; *C. boranensis*	Sixteen species of *Commiphora* predicted on climatic parameters to occur in northern Ethiopia and do not occur there

RICHNESS AND DIVERSITY OF THE ETHIOPIAN BURSERACEAE IN RELATION TO DENSITY OF OBSERVATIONS

In the Figs. 51–54, we have on a grid of one-degree squares summarized the total number of observed occurrence points (Fig. 51), the observed species richness indicated simply as the number of species in each square (Fig. 52), the observed species richness per square estimated with Jackknife resampling (Fig. 53), and Shanon-Wiener diversity per square calculated from the data in this work (Fig. 54).

The estimated richness with Jackknife resampling suggests a slightly more even representation of richness than simple richness recorded as number of species, suggesting that some squares are undercollected if we assume that equal environmental parameters in adjacent squares would produce equal number of recorded species. The method also suggests a slightly lower score for the well-collected squares, such as the one that includes

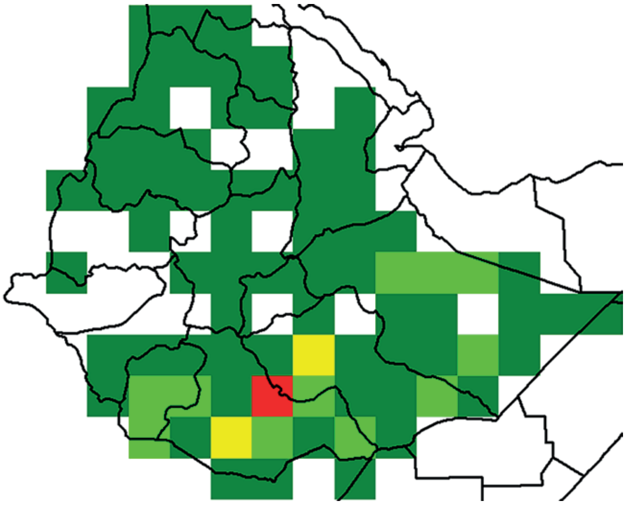


Figure 51. Number of occurrence points studied for this work (= number of locations of identified species of Ethiopian Burseraceae) on one-degree squares. Dark green: 1–20. Pale green: 21–40. Yellow: 41–60. Orange: 61–80. Red: 81–100.

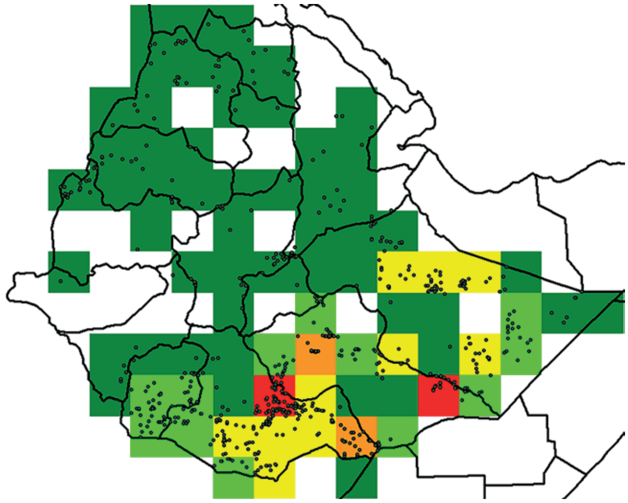


Figure 52. Observed species richness for the species of Burseraceae (richness = number of species per one-degree square), shown on one-degree squares and calculated from the data in this work. Dark green: 1–5. Pale green: 6–10. Yellow: 11–15. Orange: 16–20. Red: 21–25. The dark dots are the occurrence points.

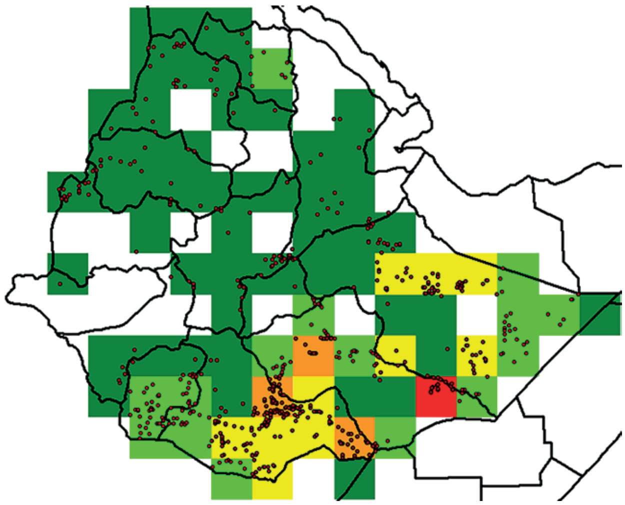


Figure 53. Expected species richness estimated with Jackknife resampling of the number of Burseraceae species per one-degree square and shown on one-degree squares. Dark green: 1–8. Pale green: 9–16. Yellow: 17–24. Orange: 25–32. Red: 33–40. The dark dots are the occurrence points.

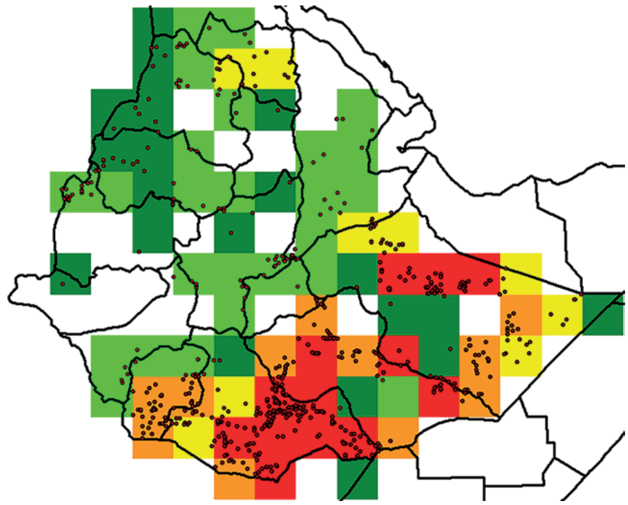


Figure 54. Shanon-Wiener diversity of the Burseraceae species per one-degree square and shown on one-degree squares. Dark green: 0.1–0.57. Pale green: 0.58–1.14. Yellow: 1.15–1.71. Orange: 1.72–2.28- Red: 2.29–3.00. The dark dots are the occurrence points.

the town of Negele, a square that is particularly well-collected.

Similarly, the calculated Shanon-Wiener diversity suggests a more evenly representation of species in the southeastern lowlands than richness simply recorded as number of species, and that the differences between the squares with regard to richness in that part of Ethiopia may be due to collecting intensity.

The collecting intensity is clearly highest around the town of Negele, lower, but still fairly high around the smaller towns of Dolo and Bogol Mayo, all three in SD; lower still to the west of Imi in BA, along the lower reach of the Webe Shebele River on the border between BA and HA, and in areas around Dire Dawa and Harar in HA, but even here higher than in the most poorly collected squares.

REVIEW OF RED-LISTED BURSERACEAE IN ETHIOPIA

In Table 4 we have summarised the general assessments made up to now and as published in the IUCN Red List of Threatened Species (https://www.iucnredlist.org/). Two species have been assessed as critically endangered, seven species as near threatened, six species as vulnerable, sixteen species as least concern, while the status of fifteen species is still unsettled.

CONCLUSIONS

The family of Burseraceae in Ethiopia includes six species of *Boswellia* and forty-two species of *Commiphora*, all either associated with deciduous woodlands and bushlands in the western lowlands of Ethiopia (*Combretum-Terminalia* woodland), the eastern lowlands (*Acacia-Commiphora* woodland and bushland and semi-desert scrub), or in the woodlands in the deep river valleys in the highlands, all vegetation types of which they form important elements. Our studies confirm that two species of *Boswellia* and one species of *Commiphora* are found in the western lowlands. Four species of *Boswellia* and forty-one species of *Commiphora* are found in the *Acacia-Commiphora* woodland and bushland and in the semi-desert scrub to the south and southeast of the highlands, mainly in the lowlands of the GG, SD, BA, and HA floristic regions according to the regions used in the Flora of Ethiopia and Eritrea, with few species in the Afar lowlands (AF). The Omo Valley forms a fuzzy border between the western and eastern groups of species. While the species of *Commiphora* are closely associated with *Acacia-Commiphora* woodland and bushland and limestone rocks or sand derived from limestone, the more detailed ecological preferences are still not clear.

To the east of the highlands and in the deep river valleys in the highlands running eastwards, fifteen species are widespread and fill their modelled climatic envelope, while sixteen have limited distributions, not filling their modelled climatic envelope (but this is also because they are represented by few collections). The latter species may be restricted to specific geological formations or be significantly undercollected, but much more collecting activity and further field studies are necessary to establish what is the reasons behind these limitations. The most narrowly distributed species are found along the southern part of the border between BA and HA, demarcated by the lower Genale and the lower Webe Shebele rivers before they enter Somalia.

The remaining seventeen species, distributed to the southeast of the highlands, have moderately wide distributions with varying climatic conditions, but do not fill their potential climatic envelope. Their ecological preferences are not yet adequately known.

Comparisons have been made of the number of observations and the richness and diversity of the species in one-degree squares. The comparisons suggest striking similarity between number of observations and richness, as well as differences between adjacent areas in which patterns of topography and climate would seem similar. Squares which are easily accessible to the travelling of plant collectors, before or now, have both higher number of observations and higher diversity than the less accessible adjacent squares. The latter must therefore be assumed to be poorly collected, particularly in the SE lowlands. Both the species that do not fill their climatic envelope and the species with irregular pattern of collecting activity make it difficult to distinguish between rare, narrow endemics and poorly collected species.

The number of independent observations (= occurrence points) of the directly observed species richness of all Ethiopian Burseraceae on one-degree squares, the species richness of *Commiphora* species on one-degree squares estimated with Jackknife, and the Shanon-Wiener diversity of *Commiphora* on one-degree squares all

Table 4. Assessment of conservation status of Ethiopian Burseraceae species in the IUCN classification units used in the IUCN Red List of Threatened Species (https://www.iucnredlist.org/). B: *Boswellia*; C: *Commiphora*. Unnamed species (only identified by reference to one or a few collections) are not listed.

Not yet red-listed	*C. paolii*; *C. myrrha*; *C. samharensis*; *C. rostrata*; *C. erosa*; *C. serrulata*; *C. gurreh*; *C. quadricincta*; *C. habessinica*; *C. kua*; *C. horrida*; *C. gileadensis*; *C. multifoliolata*	Thirteen species
Least concern	*B. rivae*; *B. neglecta*; *B. microphylla*; *C. edulis* subsp. *boiviniana*; *C. schimperi*; *C. africana*; *C. pedunculata*; *C. hildebrandtii*; *C. confusa*; *C. kataf*; *C. sphaerocarpa*; *C. mildbraedii*; *C. campestris*; *C. oddurensis*; *C. boranensis*; *C. chiovendana*	Sixteen species
Vulnerable	*B. papyrifera*; *B. pirottae*; *C. erlangeriana*; *C. guidottii*; *C. alaticaulis*; *C. cyclophylla*	Six species
Near threatened	*C. unilobata*; *C. sphaerophylla*; *C. obovata*; *C. corrugata*; *C. truncata*; *C. ciliata*; *C. hodai*	Seven species
Critically endangered	*B. ogadensis*; *C. monoica*	Two species
Data deficient	*C. staphyleifolia*; *C. ogadensis*	Two species

point to the highest values for approximately the same squares. The authors cannot give fully adequate reasons for this. The well collected squares group together with those with high species richness and diversity, and these, on one hand, cannot yet easily be fitted into a pattern with the poorly collected squares. It is to be hoped that much more even collecting activity will point to a clearer pattern of distribution in southeastern Ethiopia with regard to Burseraceae-species.

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AUTHORS' CONTRIBUTIONS

Both authors have gathered data in form of herbarium specimens, but during the later years mostly Sebsebe Demissew, who is responsible for the identity of the specimens after ca. 2020. For this work, Ib Friis has done most of the georeferencing and mapping of the species, and he has drawn the phytogeographical conclusions and produced the first draft of the manuscript. Both authors have worked on and approved the final and published version of the manuscript.

REFERENCES

Abiyu A, Bongers F, Eshete A, Gebrehiwot K, Kindu M, Lemenih M, Moges Y, Ogbazgh W, Sterck FJ. 2010. Incense Woodlands in Ethiopia and Eritrea: Regeneration Problems and Restoration Possibilities. In: Bongers F & Tenningkeit T. (eds.), Degraded Forest in Eastern Africa: Management and Restoration. Chapter 7. London, Routledge. https://www.taylorfrancis.com/books/e/9781849776400/chapters/10.4324/9781849776400-14

Bulakh M, Fiaccadori G. 2007. Incense. In: Ulig, S. (Ed.), Encyclopaedia Aethiopica. Vol. 3: 129–132. Wiesbaden, Harassowitz Verlag.

Chiovenda E. 1932. Flora Somala 2. Modena, Reale Orto Botanico.

Darbyshire I, Kordofani M, Frarag I, Candiga R, Pickering H. 2015. The Plants of Sudan and South Sudan – An annotated checklist. Kew, Royal Botanic Gardens.

Demissew S, Friis I. 2013. *Commiphora oddurensis* Chiov. and *C. suffruticosa* Teshome (Burseraceae): taxonomy, distribution, ecology and conservation status. Webbia. 68(2): 133–145. https://doi.org/10.1080/00837792.2013.849956

Demissew S, Friis I. In preparation. The Frankincense and Myrrh species of Ethiopia. A Field Guide.

Eltigani SA, Ohta C, Nakamiya R, Yokono M, Bito T, Takahashi K, Yabuta Y, Eltayeb MM, Ishihara A. 2025. Exploring Volatiles and Biological Effects of *Commiphora africana* and *Boswellia papyrifera* incense. Molecules 30(3): 499. https://doi.org/10.3390/molecules30030499

Friis I, Demissew S, Breugel P van. (2010). Atlas of the Potential Vegetation of Ethiopia. Biologiske Skrifter. 58. https://www.royalacademy.dk/Publications/Low/3607_Friis,%20Ib,%20Demissew,%20Sebsebe%20and%20van%20Breugel,%20Paulo.pdf

Friis I, van Breugel P van, Weber O, Demissew S. 2022. The Western Woodlands of Ethiopia - A study of the woody vegetation and flora between the Ethiopian Highlands and the lowlands of the Nile Valley in the Sudan and South Sudan. Scientia Danica. Series B, Biologica. 9: 1–521.

Fritsch E. 2007. Use of incense in the liturgy of the Ethiopian Orthodox Church. In: Ulig S (Ed.), Encyclopaedia Aethiopica. Vol. 3: 134–135. Wiesbaden, Harassowitz Verlag.

Gillet JB. 1991. Burseraceae. In: Polhill RM. (Ed.), Flora of Tropical East Africa. Rotterdam, AA Balkema.

Guidotti R. 1931. Gomme e resine della Zona Oddur. Rivista italiana delle essenze e profumi. 13: 228–233.

Hijmans RJ, Guarino L, Mathur P. (2012). DIVA-GIS Version 7.5. Manual. Chrome-extension://efaidnbmnnnibpcajpcglclefindmkaj/https://diva-gis.org/docs/DIVA-GIS_manual_7.pdf

IUCN Red List (2025). The IUCN Red List of Threatened Species. (https://www.iucnredlist.org/). See specific references with full citations and URLs in the text under the individual species.

Last G. 2009. The geology and soils of Ethiopia and Eritrea. In: Ash J. and Atkins J. (Eds.), Birds of Ethiopia and Eritrea - An atlas of distribution. London, Christopher Helm. Pp. 25–26.

Lissovsky AA, Dudov SV. 2021. Species-Distribution Modeling: Advantages and Limitations of Its Application. 2. MaxEnt. Biology Bulletin Reviews. 11: 265–275. https://doi.org/10.1134/S2079086421030087

Merow C, Smith MJ, Silander Jr, JA. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography (Copenhagen). 36(10): 1058–1069. https://doi.org/10.1111/j.1600-0587.2013.07872.x

Phillips SJ. 2017. A Brief Tutorial on Maxent. https://biodiversityinformatics.amnh.org/open_source/maxent/Maxent_tutorial2017.pdf

Pichi Sermolli REG. 1957. Una carta geobotanica dell'Africa Orientale (Eritrea, Ethiopia, Somalia). Webbia. 13: 15–132 & 1 map. https://doi.org/10.1080/00837792.1957.10669673

Tefera M, Chernet T, Haro W. 1996. Geological map of Ethiopia. 2. Edition. Ethiopian Ministry of Mines and the Geological Survey of Ethiopia, Addis Ababa.

Soromessa T. 2006. A new species of *Commiphora* (Burseraceae) from Ethiopia. Ethiopian Journal of Biological Sciences. 5(1): 1–8.

Thulin M. 1999. Burseraceae. In: Thulin, M. (Ed.), Flora of Somalia. Vol. 2. Kew, Royal Botanic Gardens. Pp. 183–228.

Thulin M. 2020. The genus *Boswellia* (Burseraceae) – The Frankincense Trees. Symbolae Botanicae Upsaliensis. 39: 1–149.

Volker-Saad K. 2007. Use of incense. In: Ulig S. (Ed.), Encyclopaedia Aethiopica. Vol. 3: 132–133. Wiesbaden, Harassowitz Verlag.

Vollesen K. 1985. Studies in Burseraceae of northeastern Africa. Kew Bulletin. 40: 39–76.

Vollesen K. 1989. Burseraceae. In: Hedberg I and Edwards S. (Eds.), Flora of Ethiopia [and Eritrea]. Vol. 3. Uppsala, Addis Ababa, Asmara. Pp. 442–478.

WorldClim. 2020–2025. Global climate and weather data. Historical climate data. Bioclimatic variables. Internet database: https://www.worldclim.org/data/bioclim.html.

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A synthesis of the biogeographic history of Brazil's phytogeographic domains

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Abstract. In this study, we provide a comprehensive and updated overview of the biogeographic history of several Brazilian phytogeographic domains: the Amazon Rainforest, Brazilian Atlantic Forest, Caatinga, Cerrado, Pampa, and Pantanal. We also outline the main hypotheses that were proposed to explain the distribution patterns and endemism of taxa within these domains. The tropical forests, specifically the Amazon Rainforest and the Brazilian Atlantic Forest, were likely continuous during the Eocene optimum. However, global cooling and increased aridity in the late Eocene and part of the Oligocene led to the fragmentation of these extensive tropical forests. This fragmentation resulted in the creation of the dry diagonal, which includes the Cerrado, Caatinga, Pantanal, and Chaco regions. The dry diagonal served as a geographic barrier, promoting the formation of the Brazilian Atlantic Forest to the East and the Amazon Rainforest to the West. Despite this barrier, forest corridors likely existed between these domains, playing a crucial role in the segregation of the Caatinga from the Cerrado. The Caatinga is the most recent of these domains, having formed in the early to mid-Holocene. The lineages characteristic of the Cerrado likely diversified between the Miocene and early Pliocene.

Keywords: Amazon Rainforest, Brazilian Atlantic Forest, Caatinga, Cerrado.

INTRODUCTION

Brazil is the largest country in the Neotropical region (and the fifth largest in the world), covering over 8.5 million km^2 (IBGE 2024). This vast geographic area encompasses a rich biota and is considered one of the most biodiverse countries on the planet (Fiaschi and Pirani 2009). It also includes distinct phytogeographic domains (Fig. 1) such as the Amazon Rainforest and the Brazilian Atlantic Forest (both tropical humid forests), the Cerrado (tropical savannas), the Caatinga (seasonally dry tropical forests), the Pampa (grasslands of Southern Brazil), and the Pantanal (seasonally flooded wetland) (Fiaschi and Pirani 2009; Fiaschi et al. 2016). This article aims to provide a comprehensive and updated overview of the biogeographic history

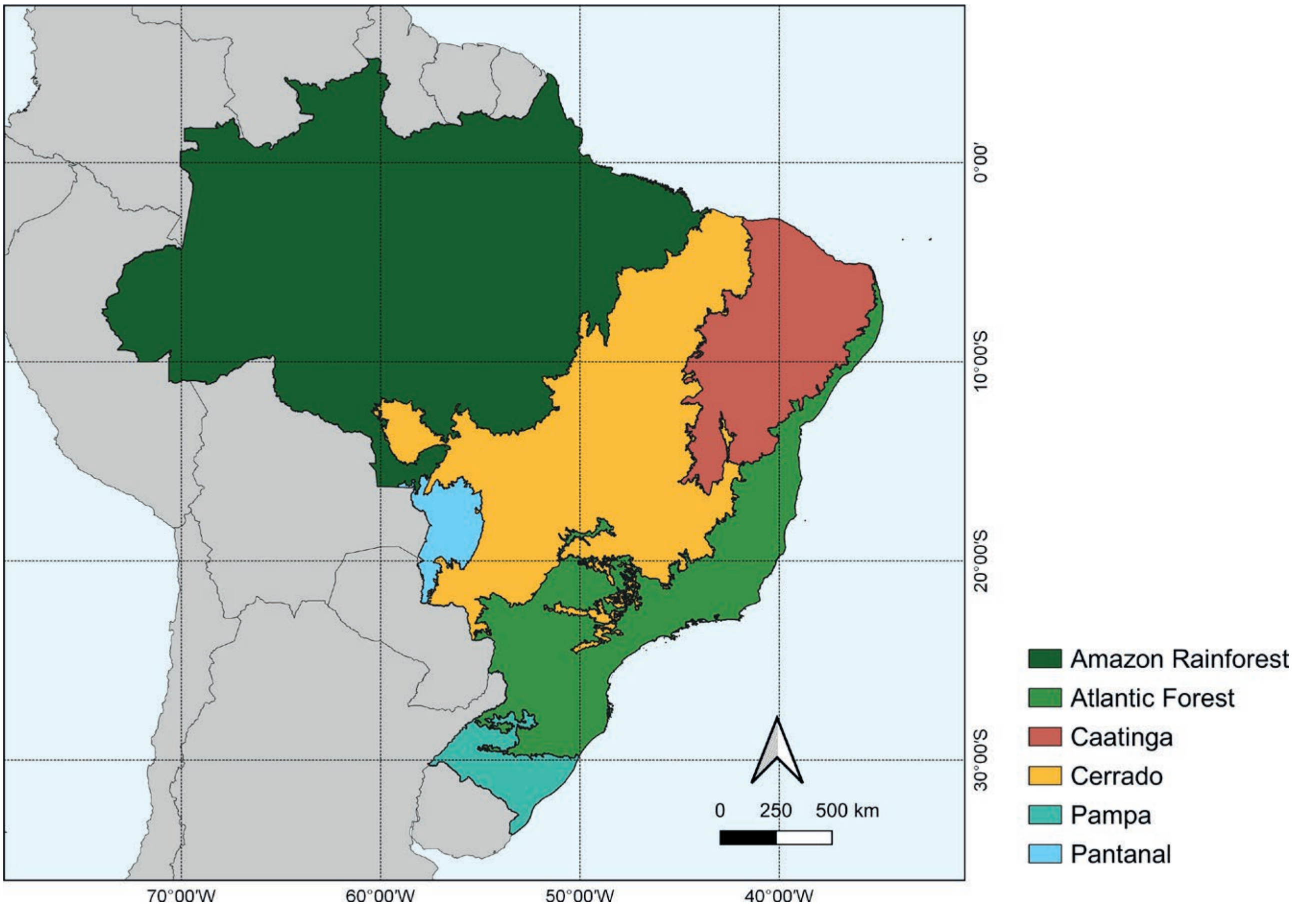

Figure 1. The phytogeographic domains of Brazil.

of these Brazilian phytogeographic domains. Additionally, we will discuss the main hypotheses that have been developed to explain the distribution patterns and endemism of species within these areas.

AMAZON RAINFOREST

The Amazon Rainforest is the largest tropical forest on the planet and one of the most biodiverse regions in the world (Nores 2020). This phytogeographic domain covers approximately 5.5 million km^2, extending from the Atlantic coast to the foothills of the Andes. It extends across nine countries, with more than half of this area located in Brazil, where it encompasses over 40% of the national territory (IBGE 2024). The Amazon Rainforest has long attracted scientific interest due to its immense biodiversity, which is home to approximately 12,800 species of vascular plants in Brazil alone (Flora do Brasil, 2020). In this sense, Antonelli et al. (2018) identified Amazon as the most important source area of species in the Neotropical region. However, the biogeographic history of this domain remains a subject of debate, with no clear consensus (Cracraft et al. 2020). Below, we present the main hypotheses proposed to explain the extraordinary biodiversity of the Amazon.

In 1969, Jürgen Haffer (geologist and ornithologist) published a study on bird distribution patterns in the Amazon, hypothesizing that climatic fluctuations during the Pleistocene could explain the observed patterns (Rull 2020). According to Haffer (l.c.), the forests were fragmented into isolated patches, or refuges, during glacial periods (which were drier/arid). On the other hand, non-forest vegetation expanded and dominated the region (Bush and Oliveira 2006; Leite et al. 2015; Fiaschi et al. 2016; Rull 2020). Thus, speciation would have occurred within these isolated refuges. During interglacial phases (more humid), the forests would have expanded and coalesced again, while non-forested areas retracted (Bush and Oliveira 2006; Leite et al. 2015; Rull 2020). This cycle is thought to have repeated multiple times throughout the Pleistocene, shaping the distribution patterns observed today (Haffer identified nine areas of endemism as potential candidates for these refugia) (Rull 2020). To support this hypothesis, Haffer used climate data from Africa during a glacial period (100 to 20 thousand years ago) to argue that the Amazon basin experienced similar arid conditions. He suggested that "seas" of savannas surrounded isolated forest "islands," creating the genetic isolation necessary for speciation (Bush and Oliveira 2006, Fiaschi and Pirani 2009). This explanation later became known as the Pleistocene refugia hypothesis.

Many studies on different groups of organisms (including butterflies, frogs, lizards, and various plant taxa) have supported the predictions of the refugia hypothesis (Fiaschi and Pirani 2009; Antonelli and Sanmartín 2011; Rull 2020). As a result, this model has become a dominant paradigm in the scientific community (Rull 2020). However, by the late 1980s, Quaternary paleoecological data began challenging this view, revealing insufficient evidence for widespread Amazonian aridity during the last glacial maximum (21 thousand years ago) (Baker et al. 2020; Rull 2020). Furthermore, palynological and paleoenvironmental modeling-based analyses have documented the Amazon rainforest's continuity and stability during this period, contradicting key predictions of the refugia hypothesis (Fiaschi and Pirani 2009; Antonelli and Sanmartín 2011; Baker et al. 2020; Rull 2020).

More recently, calibrated molecular phylogenies have provided further evidence against the hypothesis, suggesting that the diversification of many Amazonian lineages dates back to the Neogene rather than resulting from a sudden wave of Pleistocene-driven speciation (Bush and Oliveira 2006; Fiaschi and Pirani 2009; Antonelli and Sanmartín 2011; Baker et al. 2020). Another major critique argues that the proposed refugia (interpreted as centers of endemism) may be artifacts of biased sampling rather than actual historical refuges (Fiaschi and Pirani 2009; Hoorn et al. 2010; Antonelli and Sanmartín 2011). Thus, this hypothesis has been increasingly debated and rejected by many researchers (Baker et al. 2020).

Recent data show that precipitation levels during the Last Glacial Maximum in Eastern Amazonia were similar to modern values for that region, although lower than contemporary precipitation levels in Western Amazonia (precipitation decreased during periods of greater summer insolation) (Baker et al. 2020). In contrast, Western Amazonia remained as humid as it is today (precipitation increased during periods of greater summer insolation) (Baker et al. 2020). These findings highlight distinct climatic histories between Eastern and Western Amazonia (Cracraft et al. 2020).

Moreover, several studies have shown the long-term stability of tropical rainforests from Western to central Amazonia during the Quaternary (Costa et al. 2017; Baker et al. 2020; Cracraft et al. 2020). However, evidence suggests periodic expansions and contractions of forest-savanna ecotones in Southern and Eastern Amazonia (Werneck et al. 2011; Costa et al. 2017; Baker et al. 2020; Rull 2020). Episodes of forest expansion may have even created ecological corridors (forming a mosaic landscape alongside seasonally dry tropical forests in Northeastern Brazil) connecting the Amazon and the Brazilian Atlantic Forest (Baker et al. 2020). Thus, the available evidence strongly indicates that the Amazon basin was never arid during the last glacial cycle, meaning it was not fragmented by open vegetation; pollen records further confirm that most of the region has remained forested throughout this period (Colinvaux et al. 2000; Werneck et al. 2011).

Another hypothesis was proposed to explain the high biodiversity of the Amazon, known as the disturbance-vicariance hypothesis. This hypothesis suggests that the composition of the forests changed due to the dispersal and migration of montane species (particularly emphasizing the role of the Andean elevation) during the cooling period, along with a moderate reduction in precipitation and a decrease in atmospheric CO_2 during the glacial period (Baker et al. 2020; Rull 2020). During this time, there was significant competition between the taxa that were arriving from the montane environments and those that were already established in these lower areas, which may have led to specialized adaptations (Nores 2020). However, not all paleoecologists accepted this view, and Haffer's hypothesis remained more widely acknowledged (Rull 2020).

The museum hypothesis has also been considered. According to this assumption, the high Amazonian biodiversity would be explained by the stability of the forests since the Miocene. Consequently, extinction would be reduced due to high environmental stability, and there would be an accumulation of lineages over time (Rull 2020).

The river barrier hypothesis suggests that the ancestral populations of species were fragmented and isolated as the Amazon River network developed during the Neogene and early Quaternary periods, promoting allopatric speciation (Cazé et al. 2016; Rull 2020). This idea is old, dating back to 19th-century naturalists, but it was only in the 1960s that it was formalized as a hypothesis (Cazé et al. 2016; Nores 2020). Thus, it is now considered that the large Amazonian rivers and river systems formed because the elevation of the Andes produced isolation (reduction of gene flow) and differentiation of taxa due to the fragmentation of their distribution areas (Nores 2020).

The marine transgression hypothesis suggests that during the rise in sea levels (around 100 meters) between the Tertiary and Quaternary periods, the Amazon and other tropical forests became fragmented into numerous islands and archipelagos. Thus, plant and animal species would have diversified due to geographic isolation (Nores 2020). As sea levels decreased, these forests were able to expand again (Nores 2020). According to this hypothesis, we would expect a geographic coincidence between the areas of endemism and the regions that were once isolated due to the rise in sea levels (Nores 2020).

More recently, Neogene events began to be highlighted as the main drivers of Amazonian diversification, which became known as the Neogene hypothesis (Rull 2020). These events include the Andean orogeny and the closure of the Isthmus of Panama. The paradigm shift from the Pleistocene refugia hypothesis to the Neogene hypothesis was somewhat radical; however, many scholars consider that both hypotheses are not opposed and/or exclusive (Rull 2020).

In addition to historical hypotheses, some studies examined ecological factors to explain the immense diversity of the Amazon Rainforest. These factors include greater energy availability, a higher number of ecological niches, increased productivity and net primary resources, as well as greater competition and more ecological opportunities (Cracraft et al. 2020).

In general, studies indicate that many clades of Amazonian plant groups emerged between the end of the Cretaceous period and the beginning of the Paleocene, approximately 58 million years ago (Antonelli et al. 2018; Cracraft et al. 2020). The Cretaceous floras of the New World are not well understood, but some research suggests that modern plant families became established in the Paleocene and were abundant and widespread during the Eocene (Cracraft et al. 2020). Despite the various hypotheses already proposed, it seems that the Amazonian biodiversity originated from multiple drivers and mechanisms (Rull 2020), indicating a complex evolutionary history.

BRAZILIAN ATLANTIC FOREST

The Brazilian Atlantic Forest domain once covered more than 1.3 million km^2, which is approximately 15% of Brazil's national territory, from the State of Rio Grande do Norte to Rio Grande do Sul state, along the Brazilian coast (Nores 2020; IBGE 2024). The width of this domain varies significantly, expanding inland in some regions of the Southeast, Eastern Paraguay, and Argentina (Fiaschi and Pirani 2009). This domain encompasses a range of 25 degrees of latitude and reaches altitudes exceeding 2 thousand meters (Fiaschi and Pirani 2009). The Brazilian Atlantic Forest comprises areas of tropical and subtropical forests, as well as several types of smaller vegetation, such as mangroves, restingas, high-altitude fields, and rocky outcrops (Fiaschi and Pirani 2009; Peres et al. 2020; Reginato and Michelangeli 2020).

The Brazilian Atlantic Forest is recognized as a hotspot due to its high species richness (it has approximately 16,500 species of vascular plants [Flora do Brasil 2020]) (Guedes et al. 2020; Peres et al. 2020), high levels of endemism, and the growing anthropogenic threats that have increasingly reduced and fragmented the forests (Martini et al. 2007). Several biogeographic studies have been carried out in the Brazilian Atlantic Forest, mainly seeking to understand the areas of endemism (hence the greater emphasis on this topic in the discussion below). Below, we will briefly discuss these biogeographic studies.

Multiple centers of endemism, based on various groups of organisms, have been proposed for the Brazilian Atlantic Forest (Fiaschi and Pirani 2009). The number of these centers varies according to the organisms studied and the issues addressed, which influences the selection of these areas (Fiaschi and Pirani 2009). There are studies with plants, reptiles, birds, mammals, termites, and harvestmen, which point to the segregation of the Brazilian Atlantic Forest into two blocks, North and South; with the separation between these portions being located between the States of Bahia and Rio de Janeiro, respectively (Guedes et al. 2020; Peres et al. 2020). Most of the work carried out in this phytogeographic domain points to the "break/separation" around the Rio Doce valley, located in Espírito Santo state (Fiaschi and Pirani 2009; Guedes et al. 2020; Nores 2020; Peres et al. 2020; Reginato and Michelangeli 2020).

Several explanations have been proposed for the "break" observed around the Rio Doce valley. The first, and perhaps most intuitive, suggests that the Rio Doce acts as a geographic barrier, which reduces gene flow by segregating populations that reside on opposite banks of the river (Peres et al. 2020; Reginato and Michelangeli 2020). The second explanation is based on climatic factors due to the area's proximity to the Tropic of Capricorn (Peres et al. 2020; Reginato and Michelangeli 2020). The second explanation has been more accepted for plants, although it remains a topic of debate. It is noted that the rivers of the Brazilian Atlantic Forest are relatively narrow compared to those in the Amazon, making them less effective as barriers for species with high dispersal capabilities, which is typical for many plants (Peres et al. 2020).

Despite this, differences in community composition between the Northern and Southern portions of the Brazilian Atlantic Forest are supported by evolutionary studies, which have recovered entire clades that occur exclusively within each region (Fiaschi and Pirani 2009). However, the relationships between Northern and Southern lineages appear to vary considerably among taxonomic groups (Peres et al. 2020).

The Northern Brazilian Atlantic Forest extends from the State of Rio Grande do Norte to Espírito Santo state and has two centers of endemism: Pernambuco and Bahia (center and coast) (Silva et al. 2004; Fiaschi and Pirani 2009; Nores 2020). The Northern portion presents some influences from the Amazon Rainforest, thus, it is stipulated that connections occurred between these domains in the Cenozoic (Fiaschi and Pirani 2009). The Southern Brazilian Atlantic Forest, in turn, extends from the State of Espírito Santo to Santa Catarina state and has an extensive center of endemism that coincides with the Serra do Mar and Serra da Mantiqueira mountains (Silva et al. 2004; Fiaschi and Pirani 2009; Nores 2020). Taxa from the Southern portion appear to receive more influence from the Andes (Fiaschi and Pirani 2009).

The Pernambuco area of endemism was first described for birds and includes a region of evergreen, semi-deciduous, and deciduous forests along the Brazilian Atlantic Ocean coast (North of the São Francisco River, including the States of Alagoas, Pernambuco, and Paraíba) (Peres et al. 2020). This area of endemism has also been supported by plant data (Peres et al. 2020).

The area of endemism of Bahia has also been described based on bird data. This region encompasses the slopes of Chapada Diamantina, the plateaus of central Bahia, and the Northern Minas Gerais state, including evergreen, semideciduous, and deciduous forests (Martini et al. 2007; Peres et al. 2020). Data on vascular plants and butterflies also support this area of endemism (Peres et al. 2020). The coast of Bahia state, characterized by evergreen vegetation, can also be recognized as a center of endemism. It has been identified as such for several groups, including woody plants, ferns, harvestmen, and birds (Peres et al. 2020; Souza et al. 2021). In some groups of invertebrates, such as flies, harvestmen, butterflies, beetles, spiders, hemipterans, and heteropterans, this center of endemism may extend to the South bank of the São Francisco River or the North of Espírito Santo state (Peres et al. 2020).

The Serra do Mar area of endemism encompasses a habitat gradient that ranges from montane, submontane, and floodplain forests to restingas. Research on various species, including woody plants, amphibians, birds, ferns, mammals, butterflies, and snakes, supports this area of endemism (Peres et al. 2020; Souza et al. 2021; Della and Prado 2024). However, the limits of this area vary depending on the specific group being studied. For instance, for woody plants, amphibians, and birds, the area extends from the State of Santa Catarina to central Espírito Santo state. In contrast, studies focusing on vertebrates, butterflies, and snakes identify the area extending only from the State of Santa Catarina to Rio de Janeiro state. For ferns, Souza et al. (2021) defined two distinct regions: The first encompasses a small part of the Northern coast of Paraná state and the Southern coast of São Paulo state, while the second covers the Northern portion of São Paulo and Rio de Janeiro states, and a small part of the Minas Gerais state. Additionally, the Southern region of Brazil (i.e., the area that encompass the States of Paraná, Santa Catarina, and Rio Grande do Sul) has also been recognized as a center of endemism, coinciding with the occurrence of Araucaria forests, based on findings from studies involving birds, moths, butterflies, amphibians, harvestmen, and snakes.

Various hypotheses have been proposed to explain the biodiversity patterns in the Amazon Rainforest, and similar concepts have been applied to taxa from the Brazilian Atlantic Forest. In this sense, the Pleistocene refuge hypothesis has already been used to explain the areas of endemism and the distribution patterns of taxa in the Brazilian Atlantic Forest (Dantas et al. 2011; Peres et al. 2020). Paleoclimatic models suggest climate stability (with high humidity) in the Northern region of the Brazilian Atlantic Forest during the last glacial maximum (Carnaval and Moritz 2008; Peres et al. 2020) and in the areas of endemism of Pernambuco and Bahia states (Costa et al. 2017). In the Southern portion, the impact of climate fluctuations and, mainly, of the arid phases of the Pleistocene seem to have been greater (compared to the Northern region) (Carnaval and Moritz 2008). This makes the hypothesis of restricted humid refugia during glacial periods the focus of much debate (Peres et al. 2020). These models also suggest that montane species along the coast of Brazil may have expanded their ranges during cold phases of the Quaternary, despite currently having limited distributions confined to small areas (Peres et al. 2020). On the other hand, lowland taxa show signs consistent with a scenario of range contraction during colder periods (Peres et al. 2020). Fossils also indicate that the Southern Brazilian Atlantic Forest was subject to drastic climate fluctuations in the Pleistocene, which promoted the replacement of forests by fields in short periods, until the climate changed to more favorable conditions, when the forests expanded (Costa et al. 2017; Peres et al. 2020).

The river barrier hypothesis has also been considered, given the limits of areas of endemism and the North-South segregation of the Brazilian Atlantic Forest

(Dantas et al. 2011). Rivers can act as barriers, reducing gene flow, as has been verified for lizards, frogs, and snakes in the Brazilian Atlantic Forest (Dantas et al. 2011). Despite this, the rivers of the Atlantic Forest in Brazil are not as wide as those in the Amazon Forest, which questions the real role of rivers as physical barriers for many taxa with greater dispersal capacity (Peres et al. 2020). However, it is expected that the formation of river basins acted as barriers at some point in the past (Peres et al. 2020).

The neotectonic hypothesis considers that the Atlantic margin of the South American plate is tectonically passive, though changes have occurred and continue to occur, leading to the formation of faults and fractures that reshape the landscape (Dantas et al. 2011; Peres et al. 2020). The uplift of Brazil's coastal mountains (called Serra do Mar) promoted significant changes, particularly in the Southeastern region (Peres et al. 2020). Notable among these changes are shifts in precipitation that began in the Pliocene epoch, approximately 5.6 million years ago. These shifts have had a profound impact on the distribution of wet and dry habitats, contributing to the fragmentation of the Brazilian Atlantic Forest (Dantas et al. 2011).

The Serra do Mar and Serra da Mantiqueira may have acted as refuges and centers of endemism and diversification for Neotropical organisms (Guedes et al. 2020). High-altitude grasslands developed on the tops of these mountains, which share some floristic similarities with the Andean Páramos (Fiaschi and Pirani 2009; Andrade et al. 2016; Guedes et al. 2020). In these mountainous regions, the different geomorphological and climatic attributes, as well as geographic isolation, appear to influence the observed gradients in species richness today (Reginato and Michelangeli 2020). Biotic connections, or exchanges/dispersals, between the Andes and the Southeastern mountains (such as the Southern route through Patagonia) have been proposed to explain the disjunction of many taxa (Guedes et al. 2020). In addition, other explanations have been developed, such as fragmentation due to the uplift of the Andes during the Miocene, marine transgressions in the Miocene, and aridity in Patagonia and the Chaco since the end of the Miocene (Luebert et al. 2020).

The ecological gradient hypothesis considers the gradual transition between humid forests and drier vegetation (e.g., Cerrado and Caatinga) (Silva et al. 2004; Dantas et al. 2011). Thus, as each region presents distinct ecological characteristics, it is expected that different selective pressures will lead to divergence among organisms (Dantas et al. 2011). Observations of various species, including rats, birds, and snakes, indicate that their distribution correlates with specific humidity and temperature zones. This suggests that environmental gradients play a significant role in the evolution of these groups (Dantas et al. 2011). Additionally, recurrent marine progressions and introgressions in the glacial period may have significantly influenced the dynamics of the biota by promoting the isolation of certain taxa (Leite et al. 2016).

The biogeographic history of the Brazilian Atlantic Forest, as well as the Amazon Rainforest, is quite complex. As seen above, several mechanisms and events may have been responsible for generating the enormous biodiversity present in this phytogeographic domain. Despite this, we still do not have clarity about which events were most important or highlighted.

CAATINGA

The Caatinga phytogeographic domain extends over approximately 850,000 km^2 (corresponding to approximately 11% of the national territory) along the Northeastern region of Brazil (Fiaschi and Pirani 2009; Thomé et al. 2016; Silva and Souza 2018; IBGE 2024). The Caatinga comprises the largest area of seasonally dry tropical forests in the Neotropical region. This domain has approximately 5,100 species of vascular plants (Flora do Brasil 2020). It occurs on fertile soils with high nutrient content and moderate to high pH; however, it suffers from severe drought for at least five months a year (which determines its geographic distribution) (Cole 1960; Werneck 2011; Werneck et al. 2011; Thomé et al. 2016; Florentín et al. 2018; Silva and Souza 2018; Collevatti et al. 2020). The Caatinga is very different from the Cerrado, as it consists mainly of trees and thorny shrubs, which lose their leaves during the dry season; it also has succulent plants, such as cacti and bromeliads, and low-growing herbs, which emerge after the rain (Cole 1960; Pennington et al. 2000; Costa 2003; Werneck 2011; Werneck et al. 2011; Florentín et al. 2018; Reginato and Michelangeli 2020). In addition, the Caatinga vegetation is intolerant to fire (Simon et al. 2009; Azevedo et al. 2020). Within this phytogeographic domain, there are so-called "brejos de altitude", which are interpreted as enclaves of humid forest in higher areas (Costa 2003).

The floristic composition of the Caatinga shows strong links with other seasonally dry tropical forest centers in the Neotropics, such as Missiones (along the Paraguay and Paraná River basins), Piedmont (Southwestern Bolivia and Northwestern Argentina), the Caribbean coast of Colombia and Venezuela, the Andean dry valleys, and the centers located in Central America, along the Pacific coast and in Mexico; but not with the Chaco and the Cerrado (Fiaschi and Pirani 2009; Côrtes et al. 2015).

The history of the distribution of the Caatinga is poorly understood (Thomé et al. 2016); in some places, the boundaries with other phytogeographic domains are clear, and in others, there may be extensive and gradual ecotones, suggesting a state of constant flux. Thus, Prado and Gibbs (1993) proposed the inclusion of the Caatinga in the definition of seasonally dry tropical forests, and based on the distribution of tree species, they established the Pleistocene arc hypothesis. This hypothesis states that seasonally dry tropical forests formed a continuous arc throughout the Neotropics. These forests would have extended into the Amazon, infiltrating the Andean region and establishing connections with the Caribbean (Prado and Gibbs 1993). This would have happened in the Pleistocene, during the glacial period, when the climate was drier and colder; and during this period, the humid tropical forests would have contracted (Pennington et al. 2000; Caetano et al. 2008; Côrtes et al. 2015; Thomé et al. 2016; Florentín et al. 2018). Later, with the increase in temperature and humidity, this arc was fragmented and would have given rise to the various nuclei of seasonally dry tropical forests that exist today in the Neotropics (Thomé et al. 2016). Thus, the species of seasonally dry forests must have originated through vicariance (Pennington et al. 2000). This hypothesis was observed in studies with plants, bees, and lizards and was accepted for several decades (Werneck 2011).

Some authors, however, have proposed long-distance dispersal events to explain the disjunct distribution of many taxa in seasonally dry tropical forests (Caetano et al. 2008; Antonelli and Sanmartín 2011; Thomé et al. 2016). More recently, Werneck et al. (2011) and Costa et al. (2017) modeled paleoenvironments in the Neotropics and found that the distribution of seasonally dry tropical forests was further fragmented during the last glacial maximum. Thus, the previously predicted expansions of seasonally dry forests into areas now occupied by the Amazon were not confirmed (Thomé et al. 2016). Furthermore, modeling results show that the Caatinga is one of the most unstable areas in South America (Costa et al. 2017). Despite this, there are still studies that support a wide and continuous distribution of seasonally dry tropical forests in the past, such as Collevatti et al. (2020).

Pollen records indicate that in certain regions, humid tropical forests have replaced the Caatinga during multiple periods of increased humidity (Thomé et al. 2016). It seems that drought conditions, similar to those experienced today, emerged during the Holocene, which suggests the relatively recent development of this phytogeographic domain (Thomé et al. 2016; Costa et al. 2017). Furthermore, modeling studies indicate that the Caatinga only expanded during the Holocene (Werneck et al. 2011). Some authors have even proposed the formation of a humid forest corridor in the late Pleistocene, connecting the Amazon Rainforest and the Brazilian Atlantic Forest, crossing the Caatinga through the Chapada Diamantina (Thomé et al. 2016). In this case, the "brejos de altitude" would be considered remnants of this past humid tropical forest (Thomé et al. 2016).

Dated phylogenies of common lineages in South American seasonally dry tropical forests suggest an origin that predates the Pleistocene (throughout the Paleogene and Neogene) (Côrtes et al. 2015; Florentín et al. 2018). Therefore, it appears that the Caatinga does not represent a remnant of this supposedly more extensive forest existing at the last glacial maximum, as proposed by the Pleistocene arc hypothesis (Côrtes et al. 2015).

Furthermore, studies have already verified some areas of endemism in the Caatinga. For animals, eight areas are recognized: Borborema Plateau, Campo Maior Complex, Ibiapaba-Araripe Complex, Northern Sertaneja Depression, Southern Sertaneja Depression, São Francisco Dunes, Chapada Diamantina Complex, and Raso da Catarina (Werneck 2011). For plants (Fabaceae), only seven of these eight areas already highlighted are recognized, the only exception being the Borborema Plateau (Werneck 2011).

CERRADO

The Cerrado is a phytogeographic domain that covers more than two million km^2, located in Brazil (mainly in the central region), reaching Bolivia and Paraguay (Simon et al. 2009). It is the second largest domain in Brazil by land area, covering approximately 20% of the national territory, surpassed only by the Amazon Rainforest (Werneck 2011; IBGE 2024). Cerrado presents several types of vegetation, from fields (with many C4 grasses), with sparse cover of shrubs and small trees, to an almost closed forest with a height of 12 to 15 meters (Cerradão) (Pennington et al. 2000; Fiaschi and Pirani 2009; Azevedo et al. 2020; Collevatti et al. 2020; Reginato and Michelangeli 2020). Another important type of vegetation in the Cerrado is the riparian forests, found along the rivers, which contain several species of tropical forests (Pennington et al. 2000). The soil of the Cerrado is acidic and has low availability of calcium and magnesium, in addition to having high levels of aluminum, and is generally well drained (Cerrado vegetation is intolerant to flooding) (Pennington et al. 2000). Fire plays a crucial role in this ecosystem, and many plant species have developed adaptations such as thick bark and cork, xylopodia, and the ability to resprout after fire (Pennington et al. 2000). Studies have shown that the vegetation of the Cerrado had already developed these adaptations to fire even before human activity was known in the region, which demonstrates the natural origin of this phytogeographic domain (Pinheiro and Monteiro 2010).

The distribution of savannas around the world is influenced by the seasonality of precipitation (Azevedo et al. 2020). In the case of the Cerrado, various factors contribute to this seasonality, including the geography of South America, its latitudinal position, and the orientation and elevation of the Andean mountains (which determine the transport of moisture across the continent) (Azevedo et al. 2020). In addition, some authors consider that CO_2 levels may have played a critical role in the expansion of Neotropical savannas. This is because grasses cannot compete with trees under high CO_2 levels or in cases of low water stress (Azevedo et al. 2020). Over the Cenozoic era, CO_2 levels fluctuated significantly: they were high during the Paleocene, promoting the expansion of forests, decreased during the Oligocene, rose temporarily in the Miocene, and then dropped drastically in the Pleistocene (Azevedo et al. 2020).

The Cerrado is recognized as a global biodiversity hotspot (with 12,700 species of vascular plants [Flora do Brasil 2020]) due to the high number of endemic plants and the anthropogenic changes it has undergone (Simon et al. 2009, Collevatti et al. 2020). The highest levels of endemism are found along the mountains of the Espinhaço Range (Minas Gerais and Bahia) and the Chapada dos Veadeiros (Goiás) (Fiaschi and Pirani 2009). Most endemic species occur in rocky fields above 900 meters, where low, herbaceous, or shrubby vegetation predominates in sandy or stony soils (Fiaschi and Pirani 2009, Andrade et al. 2016). These mountains are ancient but have been remodeled over time, so the current elevations (500–1,700 meters) were obtained from the Upper Tertiary to the Lower Quaternary (Werneck 2011).

Within the Cerrado, open vegetation is considered older than forests (Werneck 2011). Furthermore, it is believed that the highest and most continuous plateaus (Central Plateau of Goiás and Chapada dos Guimarães) may have formed a single, large Cerrado refuge during the Pleistocene. The lower plateaus and peripheral depressions, on the other hand, should have been drier than today and could have been dominated by xeric vegetation (such as the Caatinga) or by cooler and drier vegetation (such as the Pampas and Monte) (Werneck 2011).

Many studies have developed hypotheses about the origin and diversification of Cerrado vegetation based on phylogenies of representative taxa of this domain. In this sense, Simon et al. (2009), Bouchenak-Khelladi et al. (2014), and Azevedo et al. (2020) commented that, probably, several groups of grasses and legumes originated between 32 and 25 million years ago, with most of the lineages of these families being present since the beginning of the Miocene. As for the diversification of these groups, it is estimated that it occurred between the Miocene and the beginning of the Pliocene, from 10 to 4 million years ago (Simon et al. 2009; Azevedo et al. 2020). Della and Prado (2025) found that species of the genus *Ormopteris* (Pteridaceae), which are very common in the Cerrado, are relatively recent, having emerged within the last 1.3 million years. Magri et al. (2025) discovered that *Vellozia*, a common genus in the Campos Rupestres of the Cerrado, emerged and diversified during the Oligocene, occupying the Southern region of the Espinhaço Range in the Lower Miocene.

Furthermore, evidence from charcoal particles and pollen suggests that grasses and legumes became ecologically dominant only between 4 and 8 million years ago. Thus, the idea that Cerrado lineages evolved in response to the increase in C4 grasses and fire is reinforced by the presence of adaptations to the latter (Simon et al. 2009). A time lag between the origin and expansion (dominance) of savannas in South America can also be observed (Bouchenak-Khelladi et al. 2014; Stromberg 2011; Azevedo et al. 2020).

Studies have shown that taxa characteristic of savannas (which exist worldwide) are, in general, recently derived from ancestors present in humid or dry forests (Simon et al. 2009). Since the Cerrado is delimited by several other phytogeographic domains, the Amazon Rainforest, Brazilian Atlantic Forest, Caatinga, and Chaco, these domains may have contributed to the recruitment of Cerrado lineages (Simon et al. 2009), as demonstrated by Antonelli et al. (2018). Thus, the lineages existing today in the Cerrado appear to be the product of more recent diversifications and with few endemic genera (Simon et al. 2009).

Furthermore, paleoenvironmental modeling suggests that savannas have existed since the Middle Miocene, while environmental conditions suitable for forests and open ecosystems not analogous to savannas dominated the continent in earlier times, mainly from the Paleocene onwards (Beerling and Osborne 2006; Stromberg 2011; Werneck 2011; Costa et al. 2017; Azevedo et al. 2020). This shows us that the savannas of South America are not the oldest ecosystems on the continent, as previously believed (Pinheiro and Monteiro 2010; Azevedo et al. 2020). Furthermore, molecular phylogenies show a much older origin for forest taxa; for example, the radiation of Malpighiales occurred in the mid-Cretaceous, between 112 and 94 million years ago, and the origin of palm trees around 100 million years ago (Azevedo et al. 2020). Thus, South America can be considered a land of ancient forests and relatively young savannas (Azevedo et al. 2020).

The first open vegetation in South America is believed to have emerged around the middle Eocene, in the Southern portion of the continent, as indicated by phytoliths, herbivore macrofossils, and pollen data (Azevedo et al. 2020). Furthermore, data showing the decline in CO_2 at the end of the Oligocene, which precedes the Miocene cooling, and the estimated ages for the divergence of animal clades typical of this domain, support this idea (Azevedo et al. 2020).

PAMPA

The Pampa phytogeographic domain covers an area of 176,496 km², representing 2.1% of the national territory (IBGE 2024). It occupies more than half of the state of Rio Grande do Sul and extends into Argentina and Uruguay (Roesch et al. 2009). The region is characterized by a rainy climate with no dry season, but with negative temperatures during winter (IBGE 2024). Although the Pampa domain is predominantly composed of grasslands, other phytogeographic formations are also present, such as savanna, steppe, steppic-savanna, coastal vegetation, transition areas, and patches of seasonal deciduous and semi-deciduous forests (Roesch et al. 2009; Baez-Lizarazo et al. 2023).

It is estimated that between 3,000 and 4,000 plant species occur in the Pampa (Overbeck et al. 2007; Roesch et al. 2009; Fiaschi and Pirani 2009). Despite this high diversity, the relative abundance of species is low, and around 8% are endemic (Fiaschi and Pirani 2009; Roesch et al. 2009; Baez-Lizarazo et al. 2023). The main botanical families found in the Brazilian Pampa are Poaceae, Asteraceae, Cyperaceae, Fabaceae, Apiaceae, Oxalidaceae, Verbenaceae, and Iridaceae (Roesch et al. 2009).

Studies have shown that the flora of the Pampa is generally connected to other South American vegetation formations. Baez-Lizarazo et al. (2023) found that most dispersal events into the Pampa originated from the Atlantic Forest, the Andes, the Cerrado, or the Chaco. Although the Pampa is largely dominated by grasses and other herbaceous taxa, the presence of trees and woody plants is notable, especially in riparian forests. Authors such as Rambo (1954), Cabrera (1976), and Waechter (2002) had already highlighted that part of the Pampa flora is shared with the Cerrado, the Chaco, and the Andes. Most dispersal events from these domains into the Pampa occurred during the late Miocene and from the Pliocene onward (ca. 5 mya) (Baez-Lizarazo et al. 2023). In contrast, dispersal events from the Pampa to other regions have been less frequent and are mostly concentrated in the last 2 million years (from the Pleistocene onward) (Baez-Lizarazo et al. 2023). This suggests that lineage exchange between the Pampa and these other domains is asymmetrical, with most events occurring toward the Pampa. This pattern supports the idea that the Pampa may function as a macroevolutionary sink (Baez-Lizarazo et al. 2023).

Baez-Lizarazo et al. (2023) also found that some lineages diversified within the Pampa, such as: Amaryllidaceae (*Nothoscordum*), Apiaceae (*Eryngium*), Apocynaceae (*Oxypetalum*), Asteraceae (*Perezia*, *Stenachaenium*, *Hypochaeris*, *Sommerfeltia*, *Microgyne*), Cactaceae (*Frailea*, *Parodia*, *Gymnocalycium*), Euphorbiaceae (*Croton*, *Tragia*), Iridaceae (*Herbertia*, *Cypella*, *Sisyrinchium*), Solanaceae (*Calibrachoa*, *Petunia*), Orchidaceae (*Bipinnula*), and Poaceae (*Distichlis*, *Hordeum, Nassella*). These cladogenetic events mostly occurred within the last 5 million years, with a higher concentration during the Pleistocene (the last 2.6 million years).

The results obtained by Baez-Lizarazo et al. (2023), along with fossil evidence, indicate that the herbaceous vegetation of the Pampa was present since the Middle Miocene and remained dominant until after 7 mya (Ortiz-Jaureguizar and Cladera 2006). From the Pliocene to the Pleistocene (5.32–2.58 mya), grasslands and steppes dominated the region, likely associated with a rich megaherbivore fauna and cooler, drier climatic conditions (Ortiz-Jaureguizar and Cladera 2006). Starting in the Pleistocene, macrofossil and palynological records indicate a drastic change in the taxonomic and ecological composition of the Pampa flora, with the onset of more humid and stable climatic conditions and an increase in non-grass pollen (Baez-Lizarazo et al. 2023).

Thus, the current Pampa can be interpreted as a relic of the region's drier past climates, which allowed grasses to dominate the landscape (Baez-Lizarazo et al. 2023). However, the present climate is suitable for forest development (Roesch et al. 2009; Baez-Lizarazo et al. 2023). Abiotic stress on tree growth, along with biomass consumption by fire and herbivores, has been suggested as an explanation for the absence of forest vegetation in the region (Baez-Lizarazo et al. 2023).

PANTANAL

The Pantanal phytogeographic domain covers an area of 150,355 km², representing 1.8% of the national territory (Mato Grosso and Mato Grosso do Sul states) (IBGE 2024). It comprises a predominantly flat and low-lying region, surrounded by escarpments of the edge of the Paraná Sedimentary Basin and the Serra da Bodoquena to the East, and by the Chapada dos Parecis and the Serra de Cuiabá to the North. To the South, the Pantanal is bordered by the Apa River, and to the west, it extends into Bolivia and Paraguay, with smaller portions, especially in the latter (Junk and Cunha 2016). It is recognized as the largest continuous floodplain on Earth (Alho 2008). The annual floods, due to their large extent and long duration, cause significant changes in both the biotic and abiotic environments and are essential for the existence of the Pantanal (Alho 2008). Unlike other phytogeographic domains, it is the only one whose delimitation is not based on vegetation formations or phytophysiognomies.

The origin of the Pantanal can be attributed to the sub-horizontal subduction of the Nazca Plate beneath the South American Plate between the Paleogene and Neogene periods (approximately between 66 and 2.6 million years ago) (Rocha et al. 2022). This tectonic process promoted uplift and differential subsidence of the terrain, creating a depressed area between elevated blocks, corresponding to the current sedimentary basin where the Pantanal developed (Rocha et al. 2022). The subduction movement led to the formation of faults and rift-like structures, which facilitated sediment accumulation and the subsequent formation of the floodplain (Rocha et al. 2022). Later, alternating cycles of dry and wet periods during the Late Pliocene and Early Pleistocene likely contributed to the formation of a geomorphologically complex landscape in the Upper Paraguay Basin, now occupied by the Pantanal (Junk and Cunha 2016).

The Pantanal can be considered a hypersseasonal savanna, meaning a savanna subject to prolonged flooding (Junk and Cunha 2016). Its flora is closely related to that of the Cerrado (Junk and Cunha 2016), but it also includes species from the Amazon, the Chaco, and dry forests—phytogeographic domains that border the Pantanal. Some authors consider the Pantanal to be an extension of the Chaco, a semi-arid region that spans parts of Argentina, Paraguay, and Bolivia.

The vegetation of the Pantanal includes approximately 1,900 species of phanerogamic plants (Alho 2008). There are very few endemic species in the region, and it is estimated that the 6,000 years following the last intense dry period were not sufficient to generate endemism (Junk and Cunha 2016). Furthermore, the speciation process in the Pantanal may be hindered by the flood pulse, which "forces" mobile species to move between the floodplain and the river areas, while water currents passively transport propagules—or less mobile species—from one area to another (Junk and Cunha 2016). This mobility results in constant gene flow and prevents speciation that would otherwise occur through spatial isolation of populations (Junk and Cunha 2016). Thus, it can be concluded that the flora of the Pantanal is composed of widely distributed species originating from more or less adjacent phytogeographic domains, such as the Cerrado, seasonally dry forests, the Chaco, the Amazon, and the Atlantic Forest (Pott et al. 2011).

INTEGRATING THE BIOGEOGRAPHIC HISTORY OF THESE PHYTOGEOGRAPHIC DOMAINS

Studies indicate that until the end of the Paleocene and beginning of the Eocene (i.e., until ca. 34 mya), the climate was predominantly warmer and wetter than the current one, suggesting the presence of extensive and continuous tropical forests in South America (Ortiz-Jaureguizar and Cladera 2006; Werneck 2011; Collevatti et al. 2020; Peres et al. 2020). In the Eocene, according to climate reconstructions, there were tropical temperatures in up to two-thirds of South America, indicating that tropical forests were still dominant, in addition to being more diverse than those existing in the Paleocene and Holocene (Wilf et al. 2003; Burnham and Johnson 2004; Jaramillo et al. 2006; Ortiz-Jaureguizar and Cladera 2006). During the late Eocene and Oligocene (or until the Pleistocene, when the dry diagonal would have been fully formed), global episodes of cooling and drought occurred, which favored the formation and expansion of open vegetation in the Southern and Central regions of the continent (Thode et al. 2019; Peres et al. 2020). This led to the development of a diagonal strip of open and dry vegetation, known as the South American dry diagonal (also called "the greater South American disjunction") (Werneck 2011; Lohmann et al. 2013; Fiaschi et al. 2016; Thode et al. 2019; Peres et al. 2020). Although the formation of the dry diagonal began at this time, the dominance of the Cerrado and Caatinga is much more recent.

This dry diagonal led to the formation of the Brazilian Atlantic Forest to the East and the Amazon Rainforest to the West, which thus became separated (Peres et al. 2020). Therefore, the dry diagonal may have acted as a barrier to the migration of species between these two forests, explaining the floristic differences between them (Werneck 2011; Fouquet et al. 2012; Pedro 2014; Côrtes et al. 2015; Fiaschi et al. 2016; Collevatti et al. 2020). Several phylogenetic studies show that the dry diagonal acted as a strong geographic barrier for plants and animals that occur in tropical forest domains (Côrtes et al. 2015; Azevedo et al. 2020). One example is the work of Thode et al. (2019) carried out with *Amphilophium* (Bignoniaceae), a group of Neotropical lianas. Based on a dated phylogeny, the authors found the formation of two distinct clades, one with species from the Amazon Rainforest and the other with species from the Brazilian Atlantic Rainforest, and that the estimated time of divergence of these clades coincides with the period of formation of the dry diagonal.

Despite this, several studies have suggested that the Brazilian Atlantic Forest and the Amazon Forest were reconnected several times in the past, thus seeking to explain the disjunction of the taxa (Sobral-Souza et al. 2015; Capurucho et al. 2018; Collevatti et al. 2020; Peres et al. 2020). These connections may have occurred through Northeastern Brazil, in areas currently occupied by "brejos de altitude" (Costa 2003; Capurucho et al. 2018; Peres et al. 2020), or through the riparian forests existing in the South-Central Cerrado, or even through forests associated with the Paraná and Paraguay rivers (Southern Brazil), in the latter case connecting the Brazilian Atlantic Forest to the Southeastern Amazon Forest (Costa 2000; Peres et al. 2020). These connections may have occurred at different times, with the connection between the Southern Brazilian Atlantic Forest and the Southeastern Amazon and the one through the Cerrado being the oldest (dating back to the Middle/Upper Miocene, between 16–5.3 mya); the connections through the Northeast are estimated to have occurred between the Pliocene and Pleistocene, between 5–1 mya (Capurucho et al. 2018; Nores 2020; Peres et al. 2020). Since reconstructions have shown that the Eastern Amazon suffered a more intense drought (this region appears to be less stable), it is assumed that the corridors between the Brazilian Atlantic Forest and the Amazon Forest through the Southern region were the most stable and long-lasting. Nores (2020) also hypothesized that the Tocantins, São Francisco, and Jequitinhonha Rivers may have played an important role in the connections between the Brazilian Atlantic Forest and the Amazon Forest. Furthermore, phylogenetic studies also point to the hypothesis of past contact between the Southern Brazilian Atlantic Forest and the Andean tropical forests (Peres et al. 2020).

Thus, since the Cerrado and Caatinga have a more recent origin, the migration of species from tropical forests to savannas and seasonally dry tropical forests may have shaped the high diversity of these phytogeographic domains (Collevatti et al. 2020). Antonelli et al. (2018) found that lineages adapted to drought are more likely to evolve from lineages adapted to humidity than vice versa, so there are few observed transitions from dry to humid vegetation. Fine and Lohmann (2018) commented on the possibility that humid forest taxa have developed characteristics (or adaptations) associated with dry conditions within the humid areas themselves, that is, even before migrating to these dry areas.

Modern wetter climatic conditions in Central Brazil, with periods of seasonal drought, were established in the Holocene (Pinheiro and Monteiro 2010; Collevatti et al. 2020). With the increase in humidity in the Cerrado region, the leaching process became more intense, which promoted the expansion of the Cerrados and, consequently, the retraction of tropical forests, which never recovered the rich and extensive forest cover they had during the Pliocene (Pinheiro and Monteiro 2010).

Furthermore, many paleomodeling studies have found that tropical dry forests experienced a gradual southward expansion during the Holocene, with a large gap in central Brazil, where Cerrado vegetation had already established itself (Werneck et al. 2011). However, this expansion was much smaller than that proposed by the Pleistocene arc hypothesis, and it was also more recent. The last glacial maximum was probably too dry and cold to sustain large extensions of dry forests (Werneck et al. 2011). After this expansion phase, dry forests showed small fluctuations until reaching their current distribution (Werneck et al. 2011). Humid forest corridors connecting the Amazon and Atlantic forests may likely have segregated the Caatinga from the Cerrado.

Still based on paleoenvironmental modeling and using fossil pollen, Costa et al. (2017) found high stability over the last 30,000 years in Southwestern Amazonia, the Brazilian Atlantic Forest, and parts of the Cerrado. Furthermore, the climate of Western Amazonia was probably continuously humid, supporting the presence of tropical forests, and Southeastern Brazil, in turn, was colder and drier during glacial periods. This caused the grasslands and *Araucaria* Forests to spread Northward, replacing the Brazilian Atlantic Forest and savannas at latitudes up to 20 degrees South (which retreated southward only after the glaciation) (Collevatti et al. 2020). There is also evidence that during the last glacial maximum, there were wetter conditions in parts of the Caatinga (Werneck 2011).

The history of Brazilian phytogeographic domains is quite complex, characterized by numerous hypotheses that aim to explain the significant diversity and distribution patterns of various taxa (Fiaschi and Pirani 2009). Additionally, many criticisms have been raised against these hypotheses; some have been accepted for certain taxa, whereas others have been refuted, making the biogeographic history of these domains a subject of ongoing debate (Colli-Silva and Pirani 2019). This situation highlights the need for new studies involving different groups of organisms to establish congruence in results across various taxa.

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REFERENCES

Alho CJR. 2008. Biodiversity of the Pantanal: response to seasonal flooding regime and to environmental degradation. Brazilian Journal of Biology. 68: 957–966.

Andrade BO, Bonilha CL, Ferreira PMA, Boldrini I, Overbeck GE. 2016. Highland grasslands at the Southern tip of the Atlantic Forest biome: Management options and conservation challenges. Oecologia Australis. 20: 175–199.

Antonelli A, Sanmartín I. 2011. Why are there so many plant species in the Neotropics? Taxon. 60: 403–414.

Antonelli A, Zizka A, Carvalho FA, Scharn R, Bacon CD, Silvestro D, Condamine FL. 2018. Amazonia is the primary source of Neotropical biodiversity. PNAS. 115: 6034–6039.

Azevedo JAR, Collevatti RG, Jaramillo CA, Strömberg CAE, Guedes TB, Matos-Maraví P, Bacon CD, Carrillo JD, Faurby S, Antonelli A. 2020. On the young savannas in the land of ancient forests. In: Rull V, Carnaval C (Eds.). Neotropical diversification: patterns and processes (pp. 271–298). Springer Nature Switzerland.

Baez-Lizarazo MR, Köhler M, Reginato M. 2023. A historical perspective on the biogeography of the Pampa region: imprints of time and origins of its flora. In: Overbeck GE, Pillar VDP, Müller SC, Bencke GA (Eds.). South Brazilian Grasslands. Springer, Cham.

Baker PA, Fritz AC, Battisti DS, Dick CW, Vargas OM, Asner GP, Martin RE, Wheatley A, Prates I. 2020. Beyond refugia: new insights on Quaternary climate variation and the evolution of biotic diversity in tropical South America. In: Rull V, Carnaval C (Eds.). Neotropical diversification: patterns and processes (pp. 51–70). Springer Nature Switzerland.

Beerling DJ, Osborne CP. 2006. The origin of the savanna biome. Global Change Biology. 12: 2023–2031.

Bouchenak-Khelladi Y, Slingsby JA, Verboom GA, Bond WJ. 2014. Diversification of C4 Grasses (Poaceae) does not coincide with their ecological dominance. American Journal of Botany. 101: 300–307.

Burnham RJ, Johnson KR. 2004. South American palaeobotany and the origins of neotropical rainforests. Philosophical Transactions of The Royal Society Biological Sciences. 359: 1595–1610.

Bush MB, Oliveira PE. 2006. The rise and fall of the refugial hypothesis of Amazonian speciation: a paleoecological perspective. Biota Neotropica. 6:bn00106012006.

Cabrera AL. 1976. Regiones fitogeograficas Argentina. Enciclopedia Argentina de Agricultura y jardinería, Fasc. 1, 2nd ed. II Acme, Buenos Aires.

Caetano S, Prado D, Pennington RT, Beck S, Oliveira-Filho A, Spichiger R, Naciri Y. 2008. The history of seasonally dry tropical forests in Eastern South America: inferences from the genetic structure of the tree *Astronium urundeuva* (Anacardiaceae). Molecular Ecology. 17: 3147–3159.

Capurucho JMG, Ashley MV, Ribas CC, Bates JM. 2018. Connecting Amazonian, Cerrado, and Atlantic Forest histories: paraphyly, old divergences, and modern population dynamics in tyrant-manakins (*Neopelma*/*Tyranneutes*, Aves: Pipridae). Molecular Phylogenetics and Evolution. 127: 696–705.

Carnaval AC, Moritz C. 2008. Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic Forest. Journal of Biogeography. 35: 1187–1201.

Cazé ALR, Mäder G, Nunes TS, Queiroz LP, Oliveira G, Diniz-Filho JAF, Bonatto SL, Freitas LB. 2016. Could refuge theory and rivers acting as barriers explain the genetic variability distribution in the Atlantic Forest? Molecular Phylogenetics and Evolution. 101: 242–251.

Cole MM. 1960. Cerrado, Caatinga, and Pantanal: the distribution and origin of the savanna vegetation of Brazil. The Geographical Journal. 126: 168–179.

Colinvaux PA, Oliveira PE, Bush MB. 2000. Amazonian and neotropical plant communities on glacial timescales: The failure of the aridity and refuge hypotheses. Quaternary Science Reviews. 19: 141–169.

Collevatti RG, Lima NA, Vitorino LC. 2020. The diversification of extant angiosperms in the South American dry diagonal. In: Rull V, Carnaval C (Eds.). Neotropical diversification: patterns and processes (pp. 547–568). Springer Nature Switzerland.

Colli-Silva M, Pirani JR. 2019. Biogeographic patterns of *Galipeinae* (Galipeeae, Rutaceae) in Brazil: species richness and endemism at different latitudes of the Atlantic Forest “hotspot”. Flora. 251: 77–87.

Côrtes ALA, Rapini A, Daniel TF. 2015. The *Tetramerium* lineage (Acanthaceae: Justicieae) does not support the Pleistocene Arc hypothesis for South American seasonally dry forests. American Journal of Botany. 102*:* 992–1007.

Costa LP. 2003. The historical bridge between the Amazon and the Atlantic Forest of Brazil: a study of molecular phylogeography with small mammals. Journal of Biogeography. 30: 71–86.

Costa GC, Hampe A, Ledru MP, Martinez PA, Mazzochini GG, Shepard DB, Werneck FP, Moritz C, Carnaval AC. 2017. Biome stability in South America over the last 30 kyr: inferences from long-term vegetation dynamics and habitat modelling. Global Ecology and Biogeography. 27: 285–297.

Cracraft J, Ribas CC, D'Horta FM, Bates J, Almeida RP, Aleixo A, Boubli JP, Campbell KE, Cruz FW, Ferreira M, Fritz SC, Grohmann CH, Latrubesse EM, Lohmann LG, Musher LJ, Nogueira A, Sawakuchi AO, Baker P. 2020. The origin and evolution of Amazonian species diversity. In: Rull V, Carnaval C (Eds.). Neotropical diversification: patterns and processes (pp. 225–244). Springer Nature Switzerland.

Dantas GPM, Cabanne GS, Santos FR. 2011. How past vicariant events can explain the Atlantic Forest biodiversity? In: O Grillo, G Venora (Eds.). Ecosystems Biodiversity (pp. 429–442). Intechopen.

Della AP, Prado J. 2024. Areas of endemism of Pteridaceae (Polypodiopsida) in Brazil: a first approach. Cladistics. 40: 157–180.

Della AP, Schuettpelz E, Picard K, Prado J. 2025. Was the Dry Diagonal of South America a barrier for dispersing Pteridaceae (Polypodiopsida) species between the Brazilian Atlantic Forest and Amazon Forest? Journal of Biogeography. 52: e15169.

Fiaschi P, Pirani JR. 2009. Review of plant biogeographic studies in Brazil. Journal of Systematics and Evolution. 47*:* 477–496.

Fiaschi P, Pirani JR, Heiden G, Antonelli A. 2016. Biogeografia da flora da América do Sul. In Carvalho C, Almeida EAB (Orgs.) Biogeografia da América do Sul (Pp. 214–226). GEN, Roca, São Paulo.

Fine PVA, Lohmann LG. 2018. Importance of dispersal in the assembly of the Neotropical biota. PNAS. 115: 5831.

Flora do Brasil. 2020. http://floradobrasil.jbrj.gov.br/reflora. Retrieved May 21, 2020.

Florentín JE, Arana MD, Prado DE, Morrone JJ, Salas RM. 2018. Diversification of *Galianthe* species (Rubiaceae) in the Neotropical seasonally dry forests: a case study of a mainly subshrubby genus. Plant Ecology and Evolution. 151*:* 161–174.

Fouquet A, Recoder M, Teixeira Jr M, Cassimiro J, Amaro RC, Camacho A, Damasceno R, Carnaval AC, Moritz C, Rodrigues MT. 2012. Molecular phylogeny and morphometric analyses reveal deep divergence between Amazonia and Atlantic Forest species of *Dendrophryniscus*. Molecular Phylogenetics and Evolution. 62: 826–838.

Guedes TB, Azevedo AR, Bacon CD, Provete DB, Antonelli A. 2020. Diversity, endemism, and evolutionary history of montane biotas outside the Andean region. In: Rull V, Carnaval C (Eds.). Neotropical diversification: patterns and processes (pp. 299–328). Springer Nature Switzerland.

Haffer J. 1969. Speciation in Amazonian forest birds. Science. 165: 131–137.

Hoorn C, Wesselingh FP, Ter Steege H, Bermudez MA, Mora A, Sevink J, Sanmartín I, Sanchez-Meseguer A, Anderson CL, Figueiredo JP, Jaramillo C, Riff D, Negri R, Hooghiemstra H, Lundberg J, Stadler T, Särkinen T, Antonelli A. 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. Science. 330: 927–931.

IBGE. 2024. https://brasilemsintese.ibge.gov.br/territorio.html. Retrieved January 30, 2024.

Jaramillo C, Rueda MJ, Mora G. 2006. Cenozoic plant diversity in the Neotropics. Science. 311: 1893–1896.

Junk WJ, Cunha CN. 2016. The Pantanal: a brief review of its ecology, biodiversity, and protection Status. In: Finlayson CM, Milton GR, Prentice RC, Davidson NC. (Eds.). The wetland book II: distribution, description, and conservation. Springer, Dordrecht.

Leite YLR, Costa LP, Loss AC, Rocha RG, Batalha-Filho H, Bastos AC, Quaresma VS, Fagundes V, Paresque R, Passamani M, Pardini R. 2015. Neotropical forest expansion during the last glacial period challenges the refuge hypothesis. PNAS. 3: 1008–1013.

Leite YLR, Costa LP, Loss AC, Rocha RG, Batalha-Filho H, Bastos AC, Quaresma VS, Fagundes V, Paresque R, Passamani M, Pardini R. 2016. The "Atlantis Forest hypothesis" adds a new dimension to Atlantic Forest biogeography. PNAS. 113: E2099–E2100.

Lohmann LG, Bell CD, Calió MF, Winkworth RC. 2013. Pattern and timing of biogeographical history in the Neotropical tribe *Bignonieae* (Bignoniaceae). Botanical Journal of the Linnean Society. 171: 154–170.

Luebert F, Lörch M, Acuña R, Mello-Silva R, Weigend M, Mutke J. 2020. Clade-specific biogeographic history and climatic niche shifts of the Southern Andean-Southern Brazilian disjunction in plants. In: Rull V, Carnaval C (Eds.). Neotropical diversification: patterns and processes (pp. 661–682). Springer Nature Switzerland.

Magri AR, Luebert F, Cabral A, Alcantara S, Lohmann LG, Prado J, Lopes JC. 2025. Historical biogeography of *Vellozia* (Velloziaceae) reveals range expansion in South American mountaintops after climatic cooling events and increased diversification rates after the occupation of Southern Espinhaço Province. Botanical Journal of the Linnean Society. 207: 115–127.

Martini AMZ, Fiaschi P, Amorim AM, Paixão JL. 2007. A hot-point within a hot-spot: a high diversity site in Brazil's Atlantic Forest. Biodiversity and Conservation. 16: 3111–3128.

Nores M. 2020. Avian diversity in humid tropical and subtropical South American Forests, with a discussion about their related climatic and geological underpinnings. In: Rull V, Carnaval C (Eds.). Neotropical diversification: patterns and processes (pp. 145–188). Springer Nature Switzerland.

Ortiz-Jaureguizar E, Cladera GA. 2006. Paleoenvironmental evolution of Southern South America during the Cenozoic. Journal of Arid Environments. 66: 498–532.

Overbeck GE, Müller SC, Fidelis A, Pfadenhauer J, Pillar VD, Blanco CC, Boldrini II, Both R, Forneck ED. 2007. Brazil's neglected biome: the South Brazilian Campos. Perspectives in Plant Ecology, Evolution and Systematics. 9: 101–116.

Pedro VAS. 2014. Filogeografia de anfíbios da diagonal de áreas abertas da América do Sul [Doctoral thesis, Universidade Federal do Rio Grande do Norte].

Pennington RT, Prado DE, Pendry CA. 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. Journal of Biogeography. 27: 261–273.

Peres EA, Pinto-da-Rocha R, Lohmann LG, Michelangeli FA, Miyaki CY, Carnaval AC. 2020. Patterns of species and lineage diversity in the Atlantic Rainforest of Brazil. In: Rull V, Carnaval C (Eds.). Neotropical diversification: patterns and processes (pp. 415–447). Springer Nature Switzerland.

Pinheiro MHO, Monteiro R. 2010. Contribution to the discussions on the origin of the Cerrado biome: Brazilian savanna. Brazilian Journal of Biology. 70: 95–102.

Pott A, Oliveira AK, Damasceno-Junior GA, Silva JS. 2011. Plant diversity of the Pantanal wetland. Brazilian Journal of Biology. 71: 265–73.

Prado DE, Gibbs PE. 1993. Patterns of species distributions in the dry seasonal forests of South America. Annals of the Missouri Botanical Garden. 80: 902–927.

Rambo. 1954. Análise histórica da flora de Pôrto Alegre. Sellowia 6: 9–112

Reginato M, Michelangeli FA. 2020. Bioregions of Eastern Brazil, based on vascular plant occurrence data. In: Rull V, Carnaval C (Eds.). Neotropical diversification: patterns and processes (pp. 475–494). Springer Nature Switzerland.

Rocha IS, Machado R, Santos Júnior CR, Oliveira JRS, Pessi DD, Salamuni E, Ruiz AS, Paranhos Filho AC. 2022. Bacia do pantanal revisitada: uma estrutura do tipo rifte relacionada com a migração para sul da subducção sub-horizontal dos andes entre o Paleógeno e Neógeno. Boletim Paranaense de Geociências. 80: 227–241.

Roesch LFW, Vieira FCB, Pereira VA, Schünemann AL, Teixeira IF, Senna AJT, Stefenon VM. 2009. The Brazilian Pampa: A Fragile Biome. Diversity. 1: 182–198.

Rull V. 2020. Neotropical diversification: historical overview and conceptual insights. In: Rull V, Carnaval C (Eds.). Neotropical diversification: patterns and processes (pp. 13–49). Springer Nature Switzerland.

Silva AC, Souza AF. 2018. Aridity drives plant biogeographical sub regions in the Caatinga, the largest tropical dry forest and woodland block in South America. PLoS ONE. 13: e0196130.

Silva JMC, Souza MC, Castelletti HM. 2004. Areas of endemism for passerine birds in the Atlantic forest, South America. Global Ecology and Biogeography. 13: 85–92.

Simon MF, Grether R, Queiroz LP, Skema C, Pennington RT. & Hughes, C.E. 2009. Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. PNAS. 106: 20359–20364.

Sobral-Souza T, Lima-Ribeiro MS, Solferini VN. 2015. Biogeography of Neotropical Rainforests: past connections between Amazon and Atlantic Forest detected by ecological niche modeling. Evolution and Ecology. 29: 643–655.

Souza JF, Bueno ML, Salino A. 2021. Atlantic Forest: centres of diversity and endemism for ferns and lycophytes and conservation status. Biodiversity and Conservation. 30: 2207–2222.

Stromberg CAE. 2011. Evolution of grasses and grassland ecosystems. The Annual Review of Earth and Planetary Sciences. 39: 517–44.

Thode VA, Sanmartín I, Lohmann LG. 2019. Contrasting patterns of diversification between Amazonian and Atlantic Forest clades of Neotropical lianas (*Amphilophium*, Bignonieae) inferred from plastid genomic data. Molecular Phylogenetics and Evolution. 133: 92–106.

Thomé MTC, Sequeira F, Brusquetti F, Carstens B, Haddad CFB, Rodrigues MT, Alexandrino J. 2016. Recurrent connections between Amazon and Atlantic forests shaped diversity in Caatinga four-eyed frogs. Journal of Biogeography. 43: 1045–1056.

Waechter JL. 2002. Padrões geográficos na flora atual do Rio Grande do Sul. Ciência Ambiente. 24: 93–108.

Werneck FP. 2011. The diversification of Eastern South American open vegetation biomes: historical biogeography and perspectives. Quaternary Science Reviews. 30: 1630e1648.

Werneck FP, Costa GC, Colli GR, Prado DE, Sites Jr JW. 2011. Revisiting the historical distribution of seasonally dry tropical forests: new insights based on paleodistribution modeling and palynological evidence. Global Ecology and Biogeography. 20: 272–288.

Wilf P, Cúneo NR, Johnson KR, Hicks JF, Wing SL, Obradovich JD. 2003. High plant diversity in Eocene South America: evidence from Patagonia. Science. 300: 122–125.

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Untangling the nomenclatural and botanical history of the Cuban endemic palm *Copernicia macroglossa* Schaedtler

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Abstract. The complex nomenclature of the Cuban endemic palm *Copernicia macroglossa* Schaedtler is revisited. The research involved looking into six validly published names and resulted in a revision of the lectotypification of *C.* ×*macroglossa* H.Wendl. ex Becc. (accepted name *C.* ×*escarzana* León) and a reevaluation of previous typification accounts for *C.* ×*escarzana* León, *C.* ×*burretiana* León, and *C. torreana* León.

Keywords: Arecaceae, Greater Antilles, Neotropics, Odoardo Beccari, plant systematics, typification.

INTRODUCTION

The Caribbean Islands harbor a rich taxonomic diversity of palms (~251 species in 26 genera; Dransfield et al. 2008: Table 7.1); and, within this region, Cuba has the highest number of endemic species of the Arecaceae Bercht. & J. Presl. The genus *Copernicia* Mart. ex Endl., placed in the subfamily Coryphoideae Burnett, tribe Trachycarpeae Satake, has 21 species, of which ~16 endemic species are found in this island (Moya 2021a). Among them, *Copernicia macroglossa* Schaedtler (Cuban petticoat palm) has reached the horticulture trade because of its unique morphology in which its very short-petiolate leaves form a wide skirt along the trunk when they die (Figs. 1–2). The species is a relatively common element of gardens of South Florida including Montgomery Botanical Center and Fairchild Tropical Botanic Gardens which are well-known for their unique living collections of palms.

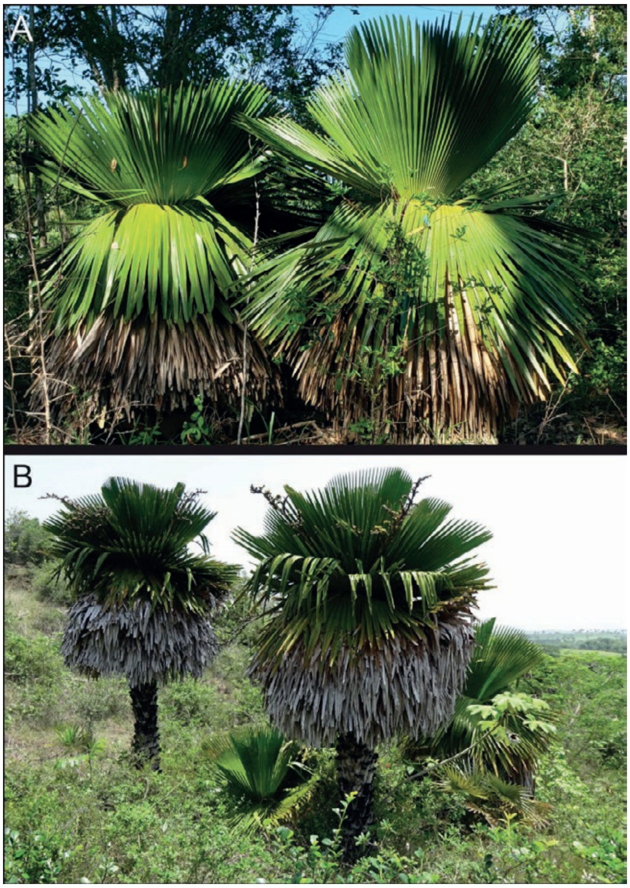

Figure 1. Individuals of *Copernicia macroglossa* in habitat. **A.** El Roque-La Cerveceria, Manacas, Santo Domingo municipality, Province of Santa Clara. **B.** Highly disturbed area in La Chivera, Minas-Bajurayabo. Guanábana municipality. Province of La Habana. Photos: Ramona Oviedo.

Figure 2. Adult individuals of *Copernicia macroglossa* in cultivation. **A.** Plant in Montgomery Botanical Center. Selvyn Valenzuela as reference. **B.** Plants with unmatured fruits in the Palmetum of Florida International University. **C.** Plant in the Palmetum of Florida International University showing the folding leaf pattern characteristic of this species. Photos: A. Vickie Murphy. B-C. Javier Francisco-Ortega.

Recently, Naranjo et al. (2025) published a "plant portrait" paper on this species, in which this name was neotypified and a detailed description was provided to clarify the vague descriptive account found in its protologue (Schaedtler 1875). When the preceding paper was prepared, it was found that not only Schaedtler's (1875) original description was ambiguous and based on juvenile plants, but that the nomenclature pertaining to this species has also been challenging and problematic. Indeed, the nomenclature history of this Cuban palm has involved six names, and it has been addressed in 13 different taxonomic publications (i.e., Sauvalle 1871; Schaedtler 1875; Beccari 1907, 1931; León 1931, 1936; Dahlgren 1936; Dahlgren and Glassman 1958, 1963; Moya et al. 2019; Moya 2021a, 2023b, 2025). Of these contributions, the most recent nomenclatural revisions were by Moya (2021a, 2023b, 2025), which provide a comprehensive account of herbarium specimens available for typifications. The preceding three works also reviewed the historical difficulties regarding the nomenclature of this name and included typification proposals. Moya's (2021a, 2023b, 2025) research led us to clarify nomenclature issues that were not previously addressed. However, we assert that Moya's (2021a, 2023b) nomenclatural assessments had a few oversights that are addressed here for the correct application of this name. The key issues pertain to the first valid publication of this species' name and subsequent type designations which we elaborate in this paper.

FROM FRANCISCO A. SAUVALLE TO GEORG SCHAEDTLER AND ODOARDO BECCARI

The name *Copernicia macroglossa* was first published by Sauvalle (1871, 1873), and he cited the author-

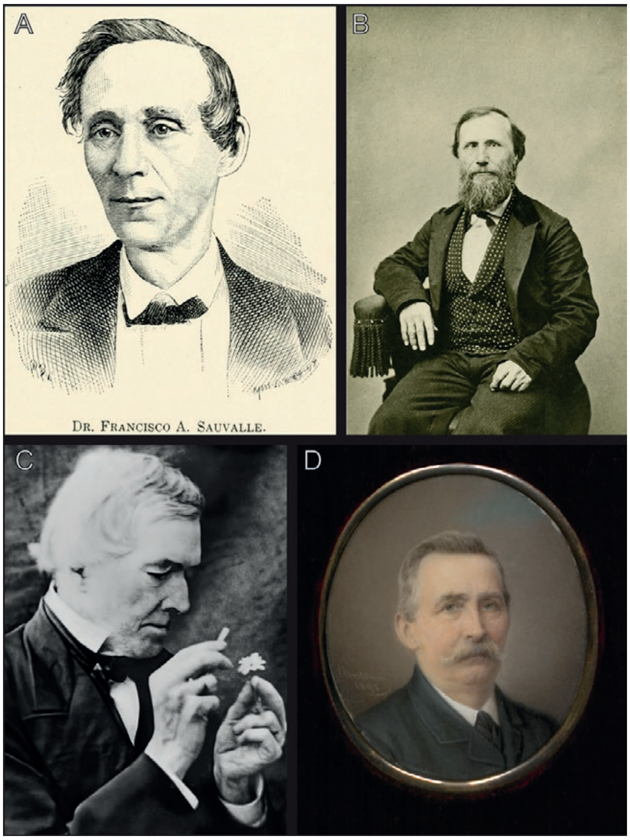

Figure 3. Naturalists involved in the early botanical history of *Copernicia macroclossa*, when it was published as an invalid name by Sauvalle (1871, 1873). **A.** Francisco Sauvalle [from Trelles (1916)], courtesy of the New York Botanical Garden. **B.** Charles Wright, courtesy of Archives of the Gray Herbarium, Harvard University. **C.** August Grisebach, courtesy of the Göttingen University Herbarium. **D.** Hermann Wendland, courtesy of the Gottfried Wilhelm Leibniz Bibliothek – Niedersächsische Landesbibliohek, Hannover, Germany.

ship as "Gris. & Wendl." Francisco A. Sauvalle (1807–1879; Fig. 3) was an American botanist who settled in Havana, Cuba in 1824, and until his death, he lived in this city (Ramos 1879; Moya 2020). The authors ascribed to this species name are two German botanists; viz., August Grisebach (1814–1879; Fig. 3) from the University of Göttingen, and Hermann Wendland (1825–1903; Fig. 3) from the Royal Gardens of Herrenhausen in Hanover. Grisebach was one of the most important plant taxonomists who worked in the Caribbean Islands (Stearn 1965), and Wendland is well known among Arecaceae specialists for his extensive contributions to the taxonomy of this plant family (Dowe 2019; Dowe et al. 2022). "*Copernicia macroglossa* Gris. & Wendl." as published by Sauvalle (1871, 1873) made reference to a specimen (number 3969) that was gathered by Charles Wright (1811–1885; Fig. 3); however, the species name was not validly published as it did not have any description or diagnosis. In this regard, the title of the article and the protologue of "*Copernicia macroglossa* Grisb. & H. Wendl." are quoted below.

> Title (vol. 5: 196. 1868): "*Flora Cubana: Revisio catalogi grisebachiani vel index plantarum cubensium ad catalogum cl: Grisebachii anno 1866 editum attemperata, pluribus Wrightianis novis speciebus aucta, valde quoque emendata, à cl: C. Wright; omnia pro Annalibus Regiae Academiae Scientiarum Havanensis digesta, nominibusque adjectis cubensibus vulgo receptis à Francisco A. Sauvalle*" [= Flora Cubana: Revision of the Grisebachian catalog or Index of Cuban plants accommodated to the catalog of the most illustrious Grisebach published in the year 1866, enlarged with many new Wrightian species, also greatly emended, by the most renowned C. Wright; all arranged for the Annals of the Royal Havana Academy of Sciences, with commonly accepted Cuban names added by Francisco A. Sauville]. Protologue: "[No.] 2368 COPERNICIA MACROGLOSSA Gris. & Wendl. ([C. Wright No.] 3969)."

The above work was published in thirty-nine parts in the journal *Anales de la Real Academia de Ciencias Médicas, Físicas y Naturales de La Habana. Revista Científica* in volumes 5–9 during 1868–1872. But eventually, Sauvalle (1873) compiled these parts together and published a single book, titled *Flora Cubana*.

It is evident from the above title, especially from the wording "[...] *pluribus Wrightianis novis speciebus aucta* [...]," and protologue, that Charles Wright is the author of the articles, that Sauvalle acted as a compiler and an editor, and that "*Copernicia macroglossa* Grisb. & H.Wendl. ex C.Wright" was not validly published.

Wright was an American botanist, and one of the most famous historical plant collectors of Cuba, wherein he travelled extensively between 1856 and 1867 (Howard 1988). Grisebach studied most of his collections, which served as the basis for the description of several Cuban endemics (Reinke 1879), and he also was in contact with Sauvalle (Moya 2021b). As a field botanist, Wright's collection numbers can be difficult to interpret as many of them are composed of two or more gatherings from different localities and therefore consist of mixed collections (Howard 1988: vii, 66, 87). Wright's unorthodox numbering system is one of the reasons that led to problems in associating the name *Copernicia macroglossa* with an appropriate specimen belonging to *C. Wright 3969*. It is worth noting, that the earliest known collection of *C. macroglossa* was made by Ramón de la Sagra (1798–1871, Fig. 4) in 1829 [Beccari 1907; *R. de la Sagra 101* (G: 00005833, photo!)] forty-two years before the name "*Copernicia macroglossa*" was proposed by Grisebach and

Figure 4. Naturalists involved in the botanical history of *Copernicia macroclossa*, between 1829 and 1931. **A.** Ramón de la Sagra, courtesy of Archivo y Biblioteca de las Cortes Generales, Madrid, Spain. **B.** Odoardo Beccari [from the frontispiece of the journal *Webbia* (volume 5, 1921)], courtesy of Centro Studi Erbario Tropicale (Herbarium FT), University of Florence, Italy, through Riccardo M. Baldini. **C.** Brother León, standing near wild plants of *C. macroglossa* at Madruga municipality, province of Mayabeque, courtesy of Division de la gestion de documents et des archives, University of Montreal, Canada.

Wendland. Ramón de la Sagra was a Spanish naturalist who lived in Cuba between 1823 and 1835, where he served as the director of the Botanic Garden of Havana in 1824 (Puig-Samper and Naranjo Orovio 2016).

Four years after Grisebach and Wendland's invalid publication of "*Copernicia macroglossa*", Schaedtler (1875: 160) validly published the name *Copernicia macroglossa*. Unfortunately, the protologue has a brief account in German and does not make mention of any precise locality. Furthermore, Schaedtler neither cited any collection nor referred to any herbarium specimen, resulting in uncertainty of the application of his species name; the translated protologue is mentioned below:

> *Copernicia macroglossa* -. The noble *Copernicia*. Without development of a stem, with disproportionately large fans, that almost arise out of the earth. It makes a more peculiar than beautiful impression through its dwarf growth with a vivid leaf-green color.[1]

Little is known about Georg Schaedtler except for an obituary which mentioned that he passed away in 1896 (Anonymous 1896) and short notes that suggest that he was based in Hannover, Germany (Schaedtler 1895; Anonymous 1896). It appears that there are no portraits of him (Dowe pers. comm.), and that he was not primarily a plant taxonomist but a horticulturist. In the same issue of this journal (i.e., *Hamburger Garten-Blumenzeitung*), he also proposed the name of a new palm genus (*Colpothrinax* Schaedtler) and the names of three new palm species (*Bactris subglobosa* Lindl. ex Schaedtler, *Colpothrinax wrightii* Schaedtler, and *Nenga pumila* H.Wendl. ex Schaedtler), and for the most part the relevant protologues show the same pattern of having brief morphological descriptions, without making a reference to herbarium vouchers or localities. As stated by Dowe (2019: 89): "Many of the [palm] names included in this publication [= *Hamburger Garten-Blumenzeitung*] were based on provisional and/or tag names provided by Wendland [...]." Because Wendland and Schaedtler worked together, Naranjo et al. (2025) interpreted the name *C. macroglossa* Schaedtler to refer to the same taxon invalidly published by Sauvalle as "*Copernicia macroglossa* Gris. & Wendl." As indicated above, Naranjo et al. (2025) not only amended Schaedtler's description but also designated a neotype for this species.

It is noted here that later works either were not aware of Schaedtler's publication of *Copernicia macroglossa* (Beccari 1907) or treated it as not validly published (Moya 2021a, 2023b). Subsequent to Schaedtler's (1875) work, Beccari (1907) published the next treatment pertinent to this Cuban palm, as he described the species "*C. macroglossa* H.Wendl. ex Becc." He coined this species name from Kerchove de Denterghem's (1878: 241) book on palms, in which "*C. macroglossa* Wendl." is mentioned without any description as part of the "Index Général" of this work. Beccari was not aware of Schaedtler's (1875) publication; nevertheless, *C. ×macroglossa* H.Wendl. ex Becc., is a later homonym and an illegitimate name (non *C. macroglossa* Schaedtler) as we discuss below. Most of the floristic studies of Cuba, as well as previous nomenclatural accounts have been using Beccari's author's name for this species (e.g., Craft

[1] German text reads as: *Copernicia macroglossa–. Die großzüngige Copernicia. Ohne Stammbildung, mit unverhältnißmäßig großen Fächern, die fast aus der Erde hervorstehen. Sie macht durch ihren zwerghaften Wuchs bei lebhafter Färbung des Blattgrüns einen mehr seltsamen, als schönen Eindruck.*

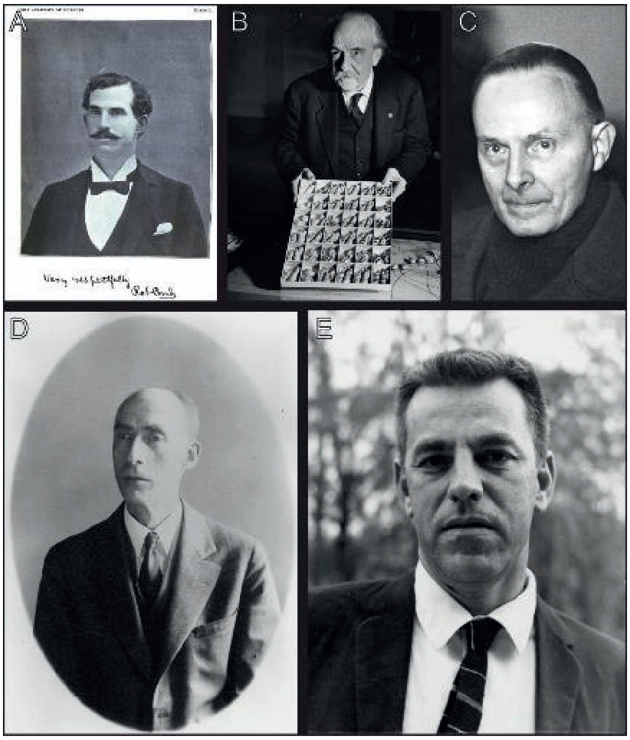

Figure 5. Naturalists involved in the botanical history of *Copernicia macroglossa*, after it was validly published by Schaedtler (1875). **A.** Robert Combs [from Pammel (1899)], courtesy of Hunt Institute *for* Botanical Documentation. **B.** Carlos de la Torre, courtesy of Smithsonian Institution Archives. **C.** Max Burret, courtesy of Library and Science History Collection, Botanic Garden and Botanical Museum Berlin. **D.** Bror Dahlgren, courtesy of Hunt Institute for Botanical Documentation. **E.** Sidney Glassman, courtesy of Hunt Institute for Botanical Documentation.

2018: 164; Moya 2021a, 2023b; Greuter and Rankin Rodríguez 2022;). The Italian botanist Odoardo Beccari (1843–1920; Fig. 4), was a recognized and prestigious tropical plant taxonomist and palm specialist (Martelli 1921); therefore, it is not surprising that his publication was rapidly accepted by Caribbean botanists and Arecaceae biologists. Beccari's description was based on three syntypes: the two aforementioned *C. Wright 3969* and *de la Sagra 101* (G: 00005833, photo!), as well as *R. Combs 335* (FI: 072423, photo!; NY: 1662393, photo!; GH: 01109341, photo!; K: 000462347, photo!). Robert Combs (1872–1899, Fig. 5), an American chemist and field botanist, made collections in Cuba during 1895 and 1896. He worked for sugar companies established on the island and, during that time, he became interested in the medicinal plants of Cuba (Combs 1897; Pammel 1899; Lanjouw and Stafleu 1954). Beccari treated *C. macroglossa* in two additional publications pertinent to Cuban palms (Beccari 1913) or in systematics of the Coryph-

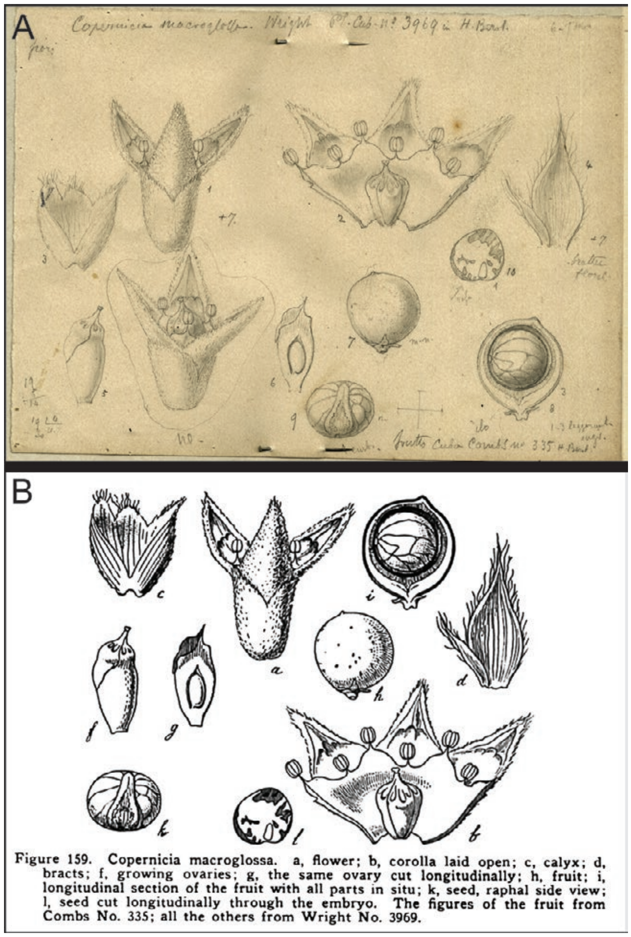

Figure 6. Illustrations of reproductive parts of *Copernicia macroglossa*. **A:** Pencil illustrations found in Beccari's herbarium (FI), courtesy of Natural History Museum Herbarium, University of Florence. **B.** Reproduction of pencil illustration shown in A as published by Beccari (1913: Fig. 159), courtesy of Harvard University Herbaria and Library.

oideae (Beccari 1931). These two accounts did not have new descriptions for the species but included illustrations with flower and fruit details (Beccari 1913: Fig. 159, 1931: Plate 25-II). These illustrations were based on pencil drawings which are housed in the Natural History Museum Herbarium, University of Florence (Fig. 6).

HERMANO LEÓN'S CONTRIBUTIONS

The French clergyman and plant taxonomist Brother [Hermano] León (1871–1955; Fig. 4) provided the next taxonomic interpretation for this species; furthermore, he was the first botanist who discussed the nomenclature issues of *Copernicia* ×*macroglossa* H.Wendl. ex Becc. (León 1931, 1936). León was a member of the De La

Salle Catholic religious order (Fratres Scholarum Christianarum), and one of the most important botanists who studied the flora of Cuba (from 1905 and his death in Havana). León developed his career as a plant taxonomist in the herbarium of the Museo de Historia Natural del Colegio "De La Salle" (LS). This museum was one with the facilities of a school that was run by De La Salle brothers in El Vedado neighborhood, Havana. After the 1959 Cuban Revolution, the LS herbarium was moved to different localities, but currently it is part of HAC (herbarium of the Instituto de Ecología y Sistemática de Cuba) collections (Regalado et al. 2008).

León had a significant understanding of the endemic flora of this island (Alain 1956; Méndez Santos 2016). As a result, after examining specimens collected by Wright and interpreting Beccari's (1907, 1913) accounts for *Copernicia macroglossa*, León (1931, 1936) assessed that Wright´s collection under number 3969 was a mixture of two *Copernicia* species differing in leaf and inflorescence traits. One part has robust-petiolate leaves armed with spines on the margin and narrow panicle-branchlets (0.3–0.8 cm in diam.). The other part exhibits short-petiolate leaves and wide panicle-branchlets (0.8–2 cm in diam.). The two other syntype collections mentioned by Beccari (i.e., *C. de la Sagra 101* and *R. Combs 335*) are of the same morphological form with wide panicle-branchlets (reviewed by Moya 2021a).

León (1931, 1936) also noticed that Beccari's (1907) description of *Copernicia macroglossa* matched the mixed collection made by Wright, as it was for a taxon with robust-petiolate leaves with spines [*picciolo corto e robusto,* [...] *fittamente armato ai margini da cima a fondo di forti spine dentiformi*; Beccari (1907: 177–178)] and with wide inflorescence branchlets defined as "thick as a little finger" [*della grossezza di un dito mignolo* (Beccari 1907: 179)].

León's (1931: 39) translated remarks for the material that he initially studied are quoted below, as they help us to understand his assessment of Wright's mixed collection:

> These observations led me to believe that Beccari's description of *Copernicia macroglossa* published in Webbia was inadvertently based on two different species. I could examine the co-type [= syntype] of Robert Combs No. 335 and of Ch. Wright No. 3969 from the Botanic Garden of New York, as well as photos of the type [= lectotype] specimens from Berlin[2]

Furthermore, León (1931: 41) stated in this taxonomic treatment:

> In the co-type [= isotype] specimen of Wright 3969, from the Torrey Herbarium of New York, the leaf is of the same species, but of the two branches of the inflorescence, one is *C. macroglossa*, and the other appears to be *C. torreana* [as *Torrena*]. This confusion on Wright's part is explainable, since it is striking that in the ten years he was in Cuba, he collected at least 4,000 gatherings. He did not indicate, many times, the locality from which they came, and it is most likely that he gathered under the same number the specimens that he believed were of the same species, although they came from different localities. It is understandable that, being palms as similar as the two we are dealing with, he could have gathered inflorescences of different species. Since this second mixture of material to which I refer does not affect the type [= lectotype], Wright 3969, from Berlin, which served as a basis for Wendland to establish the binomial "*Copernicia macroglossa*", it seems to me that said name can persist, amending Beccari's description.[3]

Based on these accounts it was clear that León (1931) studied material that was housed in B and NY, but only had access to photos of *Wright 3969* specimens housed in B. It is therefore evident from León's (1931) remarks that he: (1) found that the material housed in NY was composed of gatherings from two different species, and that he (2) was convinced that, unlike those in NY, the specimens housed in B belonged to a single homogenous gathering and pertained to a single species. He concluded that the B material was only for plants with robust-petiolate leaves armed with spines on the margin, and having narrow panicle-branchlets, and this was the material that he interpreted to be *C. macroglossa* H.Wendl. ex Becc. Specimens under *Wright 3969* that have robust-petiolate leaves and narrow inflorescence branchlets have been identified by Moya (2021a) to be hybrids between *C. macroglossa* Becc. and *C. hospita* Mart. (see further discussion in hybrids below).

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[2] Spanish text reads: *Estas observaciones me indujeron a creer que Beccari, en su descripción de la* Copernicia macroglossa *en* Webbia*, podía haber utilizado, sin darse cuenta, el material de dos especies distintas. Pude examinar los ejemplares co-tipos de Robert Combs No. 335 y de Ch. Wright 3969, del Jardín Botánico de New York, así como fotografías de los ejemplares tipos de Berlín,* [...].

[3] Spanish text reads: *En el ejemplar co-tipo de Wright 3969, del Torrey Herbarium de New York, la hoja es de la misma especie, pero de las dos ramas de la inflorescencia, una es de* C. macroglossa*, y la otra parece ser de* C. torreana [as Torreana]. *Esta confusión de Wright es explicable, pues llama la atención el hecho de que en diez años que estuvo en Cuba, haya recolectado menos de 4000* [it should read "*al menos 4000*"] *números. No indicaba, muchas veces, la localidad de donde procedían, y lo más probable es que reunía bajo el mismo número los ejemplares que creía fueran de la misma especie, aunque provinieran de localidades distintas. Se comprende que, tratándose de palmas tan parecidas como las dos de que tratamos, haya podido reunir inflorescencias de especies distintas. Como esta segunda mezcla de material a que me refiero no afecta al tipo,* Wright 3969*, de Berlín, que sirvió de base a Wendland para establecer el binomio* Copernicia macroglossa*, me parece que dicho nombre puede subsistir, enmendando la descripción de Beccari.*

León (1931) was familiar with the work of Sauvalle (1871) and knew that Wright's collection number 3969 was the material on which Wendland coined "*Copernicia macroglossa*", a palm species name that was invalidly published by Sauvalle (1871) for the first time. Therefore, León inferred that specimens of *Wright 3969*, housed in B, were examined by Wendland. Thus, León (1931: 41) concluded that because the B specimens belonged to a single gathering, then they were suitable to typify the name *Copernicia* ×*macroglossa* H. Wendl. ex Becc. as he clearly stated [translated from Spanish} "Since this second mixture of material to which I refer does not affect the type, Wright 3969, from Berlin, which served as a basis for Wendland to establish the binomial *Copernicia macroglossa*, it seems to me that said name can persist, amending Beccari's description."[4]

In conclusion, León´s (1931) interpretation of *Wright 3969* specimens found in B, led him to characterize *Copernicia* ×*macroglossa* H.Wendl. ex Becc. as *Con pecíolo robusto armada de fuertes espinas; bracteolas aovadas de 2–3 cm de largo; flores 4–5 mm de largo* (León 1931: 36) [= With robust petiole armed with strong spines; bracteoles oviform 2–3 cm in length, flowers 4–5 mm in length], and separated what he considered as non *C. macroglossa* elements (characterized as: *Sin pecíolo* [it should read "*con pecíolo my corto*", as palm leaves are always petiolate]*; bracteolas lanceoladas de 5–7 mm. de largo; flores de 6–8 mm. de largo* [= With very short petiole, bracteoles lanceolate 5–7 mm in length; flowers 6–8 mm in length]), and proposed *C. torreana* as the name of a new species and typified it with a specimen collected by him: "Lomas de la Jata, Guanabacoa (Habana), No. 14297 tipo" (see above).

As a result of these observations, León (1931: 41) chose to emend Beccari's description of *Copernicia* ×*macroglossa* and cited the name as "Copernicia Macroglossa H.Wendl. ex Becc. in Webbia 2: 177. 1907. (ex parte), emend." Thus, León's emended description applies to a hybrid, and consequently, following Moya's (2021a) research on hybrids of this species complex, we interpret in here that León's (1931) emended description pertains to a hybrid between *C. macroglossa* Schaedtler and *C. hospita*, albeit León did not treat *Copernicia macroglossa* Schaedtler as a hybrid.

León's (1931) work has two other components, which added additional complexity to this nomenclatural problem. First, he published the aforementioned *Copernicia torreana* to describe the morph with short-petiolate leaves that correspond to *C. macroglossa* Schaedtler; and secondly, he published *C.* ×*escarzana*, to account as the hybrid between *C. macroglossa* and *C. hospita*. Moya (2021a) provided an extensive taxonomic review regarding the two additional hybrid species names between *C. macroglossa* and *C. hospita*, as they (*C.* ×*burretiana* León, and *C.* ×*leoniana* Dahlgren & Glassman) were described by León (1936) and Dahlgren & Glassman (1958), respectively.

Due to inexplicable reasons, for "Copernicia Macroglossa H.Wendl. ex Becc. in Webbia 2: 177. 1907. (ex parte), emend.", León (1931) did not mention *Wright 3969* collections from B as the lectotype but cited his own gathering to lectotipify this name. Because of the citation of his collection as the type, one may argue that León created a later homonym, i.e., "*C. macroglossa* León, non H.Wendl. ex Becc. 1907)." However, it is emphasized here that León (1931: 41), in spite of emending Beccari's description, continued to cite the authorship of this taxon's name as "H.Wendl. ex Becc." In other words, although León did not refer to *Wright 3969*, his authorship citation indicates that León did not exclude Wright's collection from the Beccari name. Consequently, the Beccari name was inadvertently lectotypified by the B specimen, and León's citation of one of his collections ("Antón Recio (Sta. Clara): flores en Diciembre [*H. León and J. I. Pérez*] 14730) as the type is treated as superfluous and rejected because it was not an original material and cannot be used to typify the "H. Wendland ex Beccari name;" Furthermore, León's emended description actually pertains to a new species, viz., *C.* ×*burretiana* León (cf., Art. 7 Ex. 1) that he published later (León 1936: 208). Since León (1931) adopted the existing name *C.* ×*macroglossa* H.Wendl. ex Becc. and did not exclude its lectotype inadvertently designated by him, he did not create a later homonym (cf., Art. 48.1). Therefore, there was no "*C.* ×*macroglossa* León (1931)" and what was published as "*Copernicia burretiana* nom. nov." is corrected to "*Copernicia burretiana* sp. nov.", which is typified by León's own collection: "Antón Recio (Sta. Clara): flores en Diciembre, [H. León & J. I. Pérez] 14730." In this regard, Wendy Applequist (MO), Werner Greuter (B), John McNeill (E), and John W. Wiersema (US) were consulted, and they are of the same opinion.

Although León did not mention which specimen found in B was the actual lectotype, his reference to the photos of the B specimen does indicate the relevant material. Unfortunately among the studied material we were unable to find photos sent to León from B before 1931. For a valid publication of pre-1958 names, it was not mandatory to cite a type collection and of pre-1990 names, and it was not needed to designate a particular specimen as type (i.e., holotype); however, León explicitly mentioned that the "H. Wendland ex Beccari name" was typified by a

[4] *Como esta segunda mezcla de material a que me refiero no afecta al tipo, Wright 3969, de Berlín, que sirvió de base a Wendland para establecer el binomio* Copernicia macroglossa*, me parece que dicho nombre puede subsistir, enmendando la descripción de Beccari.*

specimen under *Wright 3969* that was housed in B and that bears robust-petiolate leaves and narrow branchlet panicles. Unfortunately, this material, along thousands of other specimens, was destroyed during the Second War World (WW2), and a new lectotype designation was needed.

It is emphasized here that extant duplicates, of the lost lectotype collected by Wright (no. 3969 p.p.), that have the same morphological traits showing robust-petiolate leaves and narrow branchlet inflorescences are isolectotypes, are eligible for a new lectotypification [duplicates listed by Moya (2021a: 17)]. It is worth mentioning that León, after he published his emended description, received three fragments from B; one of the fragments, labeled as X3 (HAC 4535), is a narrow inflorescence and is inside an envelope. The other two fragments that were mailed from B, labelled as X1 and X2 (both mounted in HAC 4536), bear thick panicle branchlets (shown in Moya 2021a: Fig. 4). Glassman (1958) was the next botanist to typify the hybrid between *Copernicia macroglossa* and *C. hospital* (= *C. ×leoniana*), having *Wright 3969* [A 00028320, 00028323 (specimen mounted in two sheets), photos!] as the type. We have selected this specimen as the lectotype of *C. ×macroglossa* H.Wendl. ex Becc.

Based on his observations on the mixed collections under *Wright 3969*, León (1931: 40), as previously mentioned, described *Copernicia torreana* as a new species to refer to the morph with shorth-petiolate leaves and wide panicle-branchlets, and he cited "*C. macroglossa* H. Wendl. ex Becc. in Webbia 2: 177, 1907. (ex parte), et in Pomona Coll. Journ. 3: 395, 1913, Fig.158" as the synonym of *C. torreana*. León cited one of his own collections ("Lomas de la Jata, Guanabacoa (Habana), [*H. León*] No. 14297 tipo") as the type; his citation did not mention a specific collection date or name of the herbarium housing this specimen. He also included several paratype collections. Subsequently, for *C. torreana*, Moya (2021a: 11) cited the type information as "Type. CUBA. [La Habana Province, Guanabacoa municipality], "Loma de la Jata, Guanabacoa, Habana," 30 Mar. 1930, *León 14297* (lectotype, [first-step]: Dahlgren 1936: 131, [second-step]: designated here, HAC ex LS 4701!" However, for the type of *C. torreana*, Dahlgren (1936: 131) merely mentioned "Torreana León, l.c. (1931) 10.– Cuba: Habana, Lomas de la Jata, Guanabacoa [León 14297]." It is evident that Dahlgren did not refer to any herbarium or date of collection; therefore, what Dahlgren (1936: 131) cited is hardly different from what was published by León (1931: 40). In contrast, for the type of *C. torreana,* Glassman (1972: 101) mentioned "Cuba: Habana (León 14297 – LS)." Although Glassman did cite the LS herbarium as housing *León 14297*, it was found that León's collection number 14297 pertains to at least four gatherings. Most of the specimens under this collection number show the date "Marzo 1930" on their labels; however, one of them (housed in F [V0092058F]) was collected in February 1930, another one (found in HAC [4698]) bears the date February 1931, and finally the fourth gathering (two specimens found in P [P725607 and P725608] have labels stating "Reçu le 15 Juin 1932". Since LS had different gatherings of *León 14297*, and because Glassman did not mention a specific date of collection, his citation is not construed here as an inadvertent act of lectotypification. In other words, neither Dahlgren (1936: 131) nor Glassman (1972: 101) did Step I process of the lectotypification of the name *C. torreana*. Therefore, it is also construed here that Moya's (2021a: 11) designation Step II process is an advertent act of lectotypification. Accordingly, Moya's (2021a: 11) citation is revised here as: Type. CUBA. [La Habana province, Guanabacoa municipality], Loma de la Jata, Guanabacoa, Habana, 30 Mar. 1930, *León 14297* (lectotype designated by Moya (2021a: 11): HAC 4701)].

In this second work, León (1936: 209) also revisited his initial assessment on his earlier typification of *Copernicia ×macroglossa* H.Wendl. ex Becc. as he had access to actual herbarium material that he received from B, and that he did not study when he published his treatment of 1931. In his second publication, León (1936) realized that B also housed a mixed collection composed of two different species under *Wright 3969*. From this 1936 work, it is asserted here that in León's mind, his 1931 concept of *C. ×macroglossa* H.Wendl. ex Becc. was incorrect as in his 1936 publication he clearly stated (translated):

> My attention was drawn to the fact that Beccari, who described *C. macroglossa* with the aforementioned material housed in Berlin, indicated that it bears flowers that are 6.5 to 7 mm. long. These dimensions match those of the flowers of *C. torreana* [*Torreana*]. As an explanation for this, I believed the Berlin Herbarium housed specimens with flowers of these two species under Wright 3969. It seems unlikely for this to happen to a collector of Wright's stature; however, it is very understandable for the reasons given in my first contribution, and for the fact that the two species are very similar in their foliage, and they often grow together within a short distance of each other. These assumptions have been confirmed by Dr. Burret, an eminent authority on the subject, who was also kind enough to send me photographs and corresponding material for verification, the binomial *Copernicia macroglossa* does not correspond to any defined species, as it is based on a double species confusion, and should be treated as "*nomen confusum*."[5]

[5] Spanish text reads: [...] *me llamó la atención el hecho de que Beccari que describió* C. macroglossa *con el arriba mencionado material de Berlín, da las flores como de 6.5 a 7 mm. de largo, dimensiones que corresponden a las flores de* C. torreana [Torreana]. *Pensé entonces que no*

It is emphasized here that based on an individual botanist's opinion, a plant name cannot be rejected as a *nomen confusum* and that a proposal to the Code Committee for a rejection of the species name, and a subsequent approval from the Code Committee are required.

León's (1936: 209) new assessment on the Berlin specimens led him to propose the aforementioned *Copernicia* ×*burretiana* as a "nom. nov." for "*Copernicia* ×*macroglossa* H.Wendl. ex Becc. emend. León," and he applied this "new name" for the plants possessing armed and robust-petiolate leaves and narrow panicle-branchlets. The same reference also provides the type citation (aforementioned collection *H. León & J. I. Pérez 14730*). Later, Dahlgren and Glassman (1963: 84) mentioned the type as "Antón Recio, Las Villas, León [& J. I. Pérez] 14730 (LS)" (sic), but without specific information on the actual sheet bearing the type.

Subsequently, Moya (2021a) designated LS.1 (housed in HAC without sheet number) as the lectotype, and this specimen label shows "H. León y J. I. Perez" as the collectors and "Diciembre 1930" as the collection date. We add that Moya (2021a) located eight specimens of *C.* ×*burretiana* from the type locality (Antón Recio) which bear the number 14730. The specimens are housed in BH, HAC, and US, and we interpret that these specimens originally belonged to the LS holdings. Of the eight specimens, six were collected in December 1930 and have "H. León and J. I. Perez" as the collectors. The remaining two specimens have only H. León as the collector and were gathered on December 23, 1930 (HAC 4538, photo!) and December 15, 1930 (BH 000038100, photo!). We do not consider these two gatherings as original material and do not treat them as isolectotypes.

CONTRIBUTIONS MADE AFTER HERMANO LEÓN'S STUDIES

León's (1931) treatment of "Copernicia Macroglossa H.Wendl. ex Becc. in Webbia 2: 177. 1907. (ex parte), emend." was not followed in the subsequent studies on the nomenclature and taxonomy of this species (e.g., Dahlgren and Glassman (1958, 1963), Moya et al. (2019), and Moya (2021a, 2023b, 2025).

Subsequent to León's studies on *Copernicia macroglossa* H.Wendl. ex Becc. and its allies, the next plant taxonomists to make significant contributions on this complex were Bror Eric Dahlgren (1877–1961; Fig. 5; Kitzke 1962) who was a Swiss born American botanist, and Sidney Frederick Glassman from USA (1919–2008; Fig. 5; Noblick 2009). Of these two authors, Dahlgren (1936: 129) indicated "Cuba [Wright 3969]" as the type for *C. macroglossa* H.Wendl. ex Becc., without citing the name of the herbarium housing the type. Since *Wright 3969* consists of a mixture, Dahlgren's citation does not constitute an act of inadvertent lectotypification of the Beccari name. Subsequently, these two authors published *C.* ×*leoniana* Dahlgren & Glassman as the name of a new species (Dahlgren and Glassman 1958: 103–105) and remarked that "León [1931, 1936] apparently intended to publish this species [= *C. leoniana*] as new; instead he published both *C.* ×*burretiana* León [as *Burretiana*] and *C. torreana* León [as *Torreana*] as synonyms of *C. macroglossa* (*Rev. Soc. Geogr. Cuba* IV, 2: 10–12. 1931; *Mem. Soc. Cubana Hist. Nat.* 10, 4; 208–209. 1936). We are describing this species in honor of Brother León, late Director of the Colegio de la Salle in Havana." It is asserted here that both Dahlgren and Glassman were partly correct about León's intention of describing a new species, but the authors erred in their remark. León (1931, 1936) published *C.* ×*burretiana* and *C. torreana* as the names of new species, but later León (1936) opted to reject the name *C. macroglossa*, because he treated this as "*nomen confusum*".

Dahlgren and Glassman (1958) assigned their intended new species name *Copernicia* ×*leoniana* to those plants with robust-petiolate leaves and narrow branchlet panicles. They were aware of the putative hybrid origin of *C.* ×*leoniana* (Dahlgren and Glassman 1963: 86); however, they did not recognize this taxon be a hybrid, as later it was suggested by Moya (2021a). They designated one specimen of *Wright 3969* housed in A (mounted in two sheets) as the type. One of the sheets shows an inflorescence in flower and young fruit [illustrated by Dahlgren and Glassman 1963: Figure 55, identified by Moya (2021a: 17) as A00028320], and the other sheet has a leaf [illustrated by Dahlgren and Glassman 1963: Figure 56, identified by Moya (2021a: 17) as A00028323].

In their second contribution, a major work on the West Indian species of *Copernicia*, Dahlgren and Glassman (1963: 84–95, 152–162) revisited their previous interpretation on *C.* ×*burretiana* and *C. torreana* and made two conclusions. Firstly, they (p. 84) treated *C.*

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había otra explicación del hecho sino la existencia en el Herbario de Berlín también, de flores de dos especies en el Nº. 3969 de Wright. Aunque esto parezca inverosímil de parte de un colector de la talla de Wright, es muy comprensible por las razones expuestas en mi primera contribución, y por el hecho de que las dos especies se parecen mucho en su follaje y a menudo crecen una a poca distancia de la otra. Como mi suposición ha sido confirmada por el doctor Burret, autoridad eminente en la materia, quien además tuvo la bondad de mandarme la comprobación en fotografias y material correspondiente, el binomio Copernicia macroglossa *no corresponde a ninguna especie definida, basado que está en una doble confusion, y debe pasar a la categoria de "*nomen confusum."

×*burretiana* as the accepted name included the following as synonyms: "*Copernicia macroglossa* Wendl. ex Becc., Webbia 2: 177. 1907, pro parte. *Copernicia macroglossa* of León, Rev. Soc. Geogr. Cuba 4: 41. 1931. *Copernicia Leoniana* Dahlgr. & Glassm., Principes 2: 103. 1958".

Secondly, they (pp. 152–153) listed *C. macroglossa* H.Wendl. ex Becc. (in Webbia 2: 177. 1907) as an accepted name and cited *C. torreana* (short-petiolate leaf individuals) as a synonym; they interpreted the Beccari name as referring to those morphs with short-petiolate leaves, and thus they inadvertently emended Beccari's (1907) description, so that it did not encompass individuals with robust-petiolate leaves.

Furthermore, Dahlgren and Glassman (1963: 153) typified *C. macroglossa* H.Wendl. ex Becc., selecting a specimen from one of *Wright 3969* gatherings housed in A that exhibits wide panicle branchlets as the lectotype ("Type: Trinidad, Las Villas, Wright 3969, in part (B, holotype [destroyed]; A, lectotype)"). Dahlgren and Glassman (1963: Figure 119, left fragment) published a photo of this specimen. During our research, we could not locate this sheet; therefore, it is regarded as misplaced or lost. Unfortunately, even if the relevant specimen were to exist, its morph (with short-petiolate leaves) is contrary to León's (1931: 40) designation of a morph comprising leaves with robust petioles. Therefore, Dahlgren and Glassman's designation is rejected.

Subsequently, Glassman (1972: 99) listed "*Copernicia macroglossa* Wendland ex Beccari, Webbia 2: 177. 1907; 1913; t. 23, 2, 1931; León, 1931; Dalgren & Glassman, 1963. – Cuba (Wright 3969 – A). *C. burretiana* León, in part, *C. torreana* León." In other words, Glassman essentially repeated what was cited Dahlgren and Glassman (1963: 152–153). Therefore, his citation does not constitute an act of lectotypification of the Beccari's name.

The last two nomenclature treatments of *Copernicia macroglossa* H.Wendl. ex Becc. were provided by Moya (2021a, 2023b). In the first of these works Moya (2021a: 10) cited "Type. "CUBA. [Sancti Spíritus province, Trinidad municipality], "Potrero Manatí," 19 Mar. 1867, *Wright 3969b*, *p. p., emend*. Moya (lectotype, [first-step]: Dahlgren 1936: 129, A, [second-step], designated here, HAC 4536 [frag. ex B!], HAC [photo of B!]." Regarding Moya's mention of "lectotype, [first-step]", as already noted, Dahlgren's (1936: 129) citation does not constitute any act of lectotype designation. With reference to Moya's designation of "HAC 4536 [frag. ex B!], HAC [photo of B!]" as the "lectotype … [second-step]", Moya's (2021a: Figure 4) shows the lectotype that he designates. It has fragments X1 (bottom) and X2 (top) of *Wright 3969* from B now at HAC (HAC 4536); the fragments X1 and X2 pertain to thick inflorescence, and thus Moya's designation is in conflict with León's (1931) emended description of *C. macroglossa* H.Wendl. ex Becc. Therefore, Moya's (2021a) lectotype designation is rejected.

In his second work, Moya (2023b: 5) mentioned that he was correcting his previous lectotypification ("Here, I correct my error in Moya (2021) when I discussed *Copernicia macroglossa* Becc., when it should be *Copernicia macroglossa* H. Wendl. ex Becc"); he abandoned his previous lectotype citation and relectotypified the name *Copernicia macroglossa* H.Wendl. ex Becc. as: "Type. CUBA. Sancti Spíritus province, Trinidad municipality, "Potrero Manatí," 19 Mar. 1867, *C. Wright 3969*, p. p. B, emend. Moya (lectotype, [first-step]: Dahlgren and Glassman 1963: 153, A*, [second-step]: designated here, GH00028326." As mentioned above, Dahlgren and Glassman's (1963: 153, Figure 119, left specimen) designation pertains to a morph (with wide branchlets), which is contrary to León's (1931: 40) designation of a morph comprising narrow inflorescens. Likewise, Moya's (2023b) designation is also contrary to León's (1931: 40) designation.

In conclusion, in our assessment of the type of *Copernicia macroglossa* H.Wendl. ex Becc. emend. León, we believe that the type citations by Dahlgren and Glassman (1963) and by Moya (2021a, 2023b) are erroneous, and as indicated above, much earlier León (1931) inadvertently lectotypified this name, based on the destroyed material found in B (*Wright 3969*) that has armed petioles and narrow panicle branchlets, that corresponds to a hybrid of *C. macroglossa* Schaedtler, and *C. hospita*. A new (aka substitute) lectotype designation is needed to define the taxonomic application of the name *Copernicia macroglossa* H.Wendl. ex Becc. emend. León (1931), and we herewith designate a new lectotype here.

It is emphasized here that none of the pre-Naranjo (2025) publications, such as Beccari (1907, 1913, 1931), León (1931, 1936) Dahlgren (1936), Dahlgren and Glassman (1958, 1963), Glassman (1972), Greuter and Rankin (2022), and Moya (2020, 2021, 2023) were aware that prior to Beccari's (1907) publication, Schaedtler (1875) had validly published the name *Copernicia macroglossa* and that the Beccari (1907) name was a later homonym and illegitimate, when published. In order to solve this nomenclature problem, as indicated above, Naranjo et al. (2025): (1) designated HAC 4536 (fragment "X1.") as the neotype of *C. macroglossa* Schaedtler, and (2) emended the vague description provided by Schaedtler (1875) with the description provided by Dahlgren and Glassman (1963) for *C. macroglossa* H.Wendl. ex Becc., this description is for the taxon with short petioles and wide branchlet panicles.

Since *C. macroglossa* Schaedtler and *C.* ×*macroglossa* H.Wendl. ex Becc. emend. León (1931), refer to different taxa, the latter name, an illegitimate later homonym, is treated here as a synonym of *C.* ×*escarzana* León as we elaborate below.

One of the most important components of Moya's (2021a) work was to clarify which of the published names refer to hybrids between *Copernicia macroglossa* and the Cuban endemic *C. hospita* Mart. This is relevant to understand the taxonomy of *C. macroglossa* since these two species have overlapping distribution ranges (León 1931; Moya 2021a, 2023a). León's (1931: 42–44, 46, 57–59) treatment for the genus in Cuba noticed rampant hybridization among species of *Copernicia* and based on his field observations he described *Copernicia* ×*escarzana* for a locality from the province of Sancti Spiritus where these two species grow together. León cited two syntypes for this name, and Dahlgren and Glassman (1963) designated *León 14921* as the type; later, Moya (2021a) selected a specimen of this collection housed in HAC (4574) as the lectotype. A total of seven duplicates of this specimen were located by Moya (2021a). Most of them, including the lectotype, were collected on June 27, 1931. One of them does not have a date (HAC ROIG 5873) and another was collected on June 26, 1931 (NY 00071157). We have tentatively identified them as "likely isolectotypes," as we have assumed that there were typographic errors or inadvertently had missing dates when León wrote their labels. However, under *León 14921* there is a specimen housed in F (V0092043F) reported as collected on July 31, 1930, that we interpret not to be an isolectotype. Based on extensive fieldwork and the study of herbarium material, Moya (2021a) suggested that *C.* ×*burretiana, Copernicia* ×*escarzana*, and *C.* ×*leoniana* as well as the robust-petiolate specimens collected under *Wright 3969* are the same taxon, they are hybrids of *C. macroglossa* and *C. hospita*. We concord with this interpretation, because *C.* ×*escarzana* is the earliest legitimately published name, it is the accepted one for this hybrid species. Therefore, here we also interpret *C.* ×*macroglossa* H.Wendl. ex Becc. as a name emended by León (1931), also to be as a hybrid of these two species.

Thus, following León's (1931) nomenclature treatment and his emended description, *C.* ×*macroglossa* H.Wendl. ex Becc. is the correct name for the species described by Beccari (1907) that has been in the center of the nomenclature complexity of this Cuban palm.

NOMENCLATURE DIAGNOSES[6]

Copernicia Mart. ex Endl., Gen. Pl. 4: 253. 1837.

Type: Designated by Beccari (1907: 142): *Copernicia cerifera* (Arruda) Mart., Hist. Nat. Palm. 3(7): 242 (1838); basionym: *Corypha cerifera* Arruda in H.Koster, Trav. Brazil: 494 (1816). [= *Copernicia prunifera* (Mill.) H.E. Moore].

The generitype of *Copernicia* was not listed either in the *Index Nominum Genericorum* (https://naturalhistory2.si.edu/botany/ing/; accessed on 23rd June 2023) or in the *Names in Current Use for Extant Plant Genera* (Greuter et al. 1993) or in "NCU-3e, Names in current use for extant plant genera, Electronic version 1.0" (https://www.bgbm.org/scripts/asp/IAPT/ncugentry.asp?name=Copernicia; accessed on 23rd June 2023). Subsequently, after receiving the typification information from Gandhi and Francisco-Ortega, the ING added the type details (https://naturalhistory2.si.edu/botany/ing/; accessed on 27th June 2023). Although Arruda's treatment mostly pertains to economic botany, it does have a few descriptive characters for validity of the name (Koster 1816). The genus is dedicated to the Prussian scientist and astronomer Nikolaus Kopernikus (1473–1543) who advocated for the heliocentric planetary system (Burkhardt 2016: C-52).

Copernicia macroglossa Schaedtler, Hamburger Garten-Blumenzeitung 31: 160. 1875.

[descr. emend. Franc.-Ort. & Gandhi, Curtis's Bot. Mag. 42(1). 2005 (published online on 14 May 2025 [https://doi.org/10.111/curt.12628]); B.E. Dahlgren & S.F. Glassman, Gentes Herb. 9: 152 (1963), non *Copernicia* ×*macroglossa* H.Wendl. ex Becc. (pro sp.), Webbia 2: 177 (1907); descr. emend. León, Rev. Soc. Geogr. Cuba 4(2): 41 (1931), *nom. illeg.*].

Type: *C. Wright 3969* (HAC, 4536, fragment "X1.," inside envelop, photo!), neotype designated by Naranjo et al. (2025: 9 [https://doi.org/10.111/curt.12628]; published online: 14 May 2025); isoneotypes: BRU (00054980, photo!), F (0092049.1, photo!; 0092049.2, photo!), FI (072424, photo!); GH (00028325, photo!; 00028326; photo!, 00028327; photo!; 00028328, photo!; 00028329, photo!), HAC (4536, fragment "X2," inside envelop, photo!); K (000209133, photo!; 000209134, photo!; 000462348,

[6] Accepted names are indicated in bold font.

photo!), NY (00071177, photo!; 1662386, photo!; 1662387 photo!), P (00725593, photo!; 00725594, photo!; 00725595, photo!).

Etymology and distribution

See Naranjo et al. (2025).

(=) *Copernicia torreana* León, Revista Soc. Geogr. Cuba 4: 40. 1931.

Type: Loma de la Jata, Guanabacoa, Province of La Habana, *H. León 14297*, March ["marzo"], 1930 [(HAC, 4701, photo!), lectotype designated by Moya (2021a: 10); isolectotypes: A (00028336, photo!; 00028337, photo!), F (V0092058F, photo!; V0092062F, photo!), HAC (LS-1, photo!; LS-2, photo!), MT (00116902.1, photo!; 00116902.2, photo!), NY (1662384, photo!), P (00725606, photo!, P 00725607 [likely isolectotype, no date in specimen], photo!; 00725608 [likely isolectotype, no date in specimen], photo!), S (S-R-1239, photo!), US (00087483, photo!; 00087484, photo!; 00087485, photo!; 00087486, photo!)].

Etymology

According to León (1931: 39) it honors Carlos de la Torre (1858–1950; Fig. 5) who was a distinguished naturalist and malacologist from Cuba (Secada Cárdenas et al. 2015).

(=) *Copernicia ×macroglossa* sensu Dahlgren & Glassman (1963: 152), non H. Wendl. ex Becc. (*pro sp.*), Webbia 2: 177 (1907); descr. emend. León, (1931).

Copernicia ×escarzana León, Revista Soc. Geogr. Cuba 4: 42 (1931) [*C. hospita* × *C. macroglossa*].

Type: Near the Bahía de Macío in the southeast of Trinidad, Province of Sancti Spíritus, *H. León 14921*, June ["junio"] 27, 1931 [(HAC 4574, photo!), lectotype: first-step, designated by Dahlgren and Glassman (1963: 145); second-step, designated by Moya (2021a: 15), HAC 4574, photo!; isolectotypes: BH (000038951), HAC (ROIG 5873 [likely isolectotype, no date in specimen], photo!), MT (00116888, photo!), NY (00071157 [likely isolectotype, date: June 26, 1931], photo!; 00071158, photo!; 00071159, photo!), P (00725584, photo!)].

Etymology

It appears that the epithet refers to Francisco Escarza (León, 1931: 41) who was the superintendent of the sugar mill known as Central Cieneguita, and likely one of the sons of Sotero Escarza Urioste (1831–1907; Anonymous sine die). The latter was from Spain and founded one of the best-known sugar mills of Cuba, Ingenio Portugalete, located in Batey, province of Cienfuegos (Lapique Becali and Segundo Arias 2011: 200–202). The Cienaguita mill was also located in Batey, and it was in operation between 1837 and 1928 (Lapique Becali and Segundo Arias 2011: 128–129).

Distribution

Moya et al. (2019: Figs. 7–8) identified eight localities where this hybrid species occurs. They are found in the provinces of Camagüey, Ciego de Ávila, Cienfuegos, Matanzas, Sancti Spíritus.

(=) *Copernicia ×macroglossa* H.Wendl. ex Becc. (*pro sp.*), Webbia 2: 177. 1907, non Schaedtler (1875).

[descr. emend. León, (1931): 41, *nom. illeg.* non *C. macroglossa* Schaedtler (1875)].

Type: 'Cuba. Nell'Erbario di Berlino si trovano assai completi esemplari con fiori e frutti giovani delle "Plantae Cubenses Wrightianae" n.° 3969, ed altri con frutti maturi "di Rob Combs: Flora Cubana, Province of Santa Clara, district of Cienfuegos n.° 335, *Calicita* 1895". Ho visto inoltre nell'Erbario de Candolle un esemplare raccolto nel 1829 da Ramon de la Sagra, col nome volgare di "Jata" e la nota "feuilles en spirale"'[7]. Lectotype designated by León (1931: 41; as "Como esta segunda mezcla de material a que me refiero no afecta al tipo, Wright 3969, de Berlín, que sirvió de base a Wendland para establecer el binomio, *Copernicia macroglossa*, me parece que dicho nombre puede subsistir, enmendando la descripción de Beccari."[8]): *C. Wright 3969* (B; lost in WW II); new (aka) substitute lectotype here designated: A (2 sheets): A 00028320, 00028323, photos!); isolectotypes: BR (U00054979), F (V0092050F, photo!), GH (00028321, photo!; 00028322, photo!; 00028324, photo!), HAC (4535, fragment "X.3" inside envelop, photo!), K (000209135, photo!; 000209136, photo!; 000209137), NY (00071175, photo!; 00071178, photo!; 1662385, photo!; 1662390, photo!; 1662391, photo!), P (00725596, photo!; 00725597photo!), US (00016510, photo!; 00989863, photo!).

[7] Text translates as: 'In the Berlin Herbarium there are very complete specimens with flowers and young fruits of the "Plantae Cubenses Wrightianae" No. 3969, and others with mature fruits "from Rob Combs: Flora Cubana, Province of Santa Clara, district of Cienfuegos No. 335, *Calicita* 1895". I have also seen in the Candolle Herbarium a specimen collected in 1829 by Ramon de la Sagra, with the common name of "Jata" and the note "feuilles en spirale"'.

[8] Text translated in Note 4.

Note

The designated lectotype and isolectotypes correspond to the holotype and isotypes of the name *Copernicia ×leoniana* Dahlgren & Glassman (1958).

Etymology

See Naranjo et al. (2025).

(=) *Copernicia ×burretiana* León (*pro sp.*), Mem. Soc. Cub. Hist. Nat. ''Felipe Poey" 10: 208. 1936.

Type. Palm savannah near Antón Recio, Province of Cienfuegos, *H. León and J. I. Pérez 14730*, December [*diciembre*], 1930 [(HAC LS.1, photo!), lectotype: first-step, designated by Dahlgren and Glassman (1963: 84); second-step, designated by Moya (2021a: 16), HAC LS.1, photo!; isolectotypes: HAC (EEAB s.n., photo!; LS.2, photo!; LS 4534, photo!; ROIG 5427 [likely isolectotype, no date on specimen], photo!), US (00087491, photo!)].

Etymology

According to the protologue, the epithet honors Max Burret (1883–1964; Fig. 5), who was a distinguished German botanist and palm specialist (Potztal 1959), who also studied Cuban palms (Burret 1929).

(=) *Copernicia ×leoniana* Dahlgren & Glassman (*pro sp.*), Principes 2: 103. 1958.

Type: Potrero Manatí, Province of Santi Spiritus, *C. Wright 3969* [p.p. emend. Dahlgren & Glassman (1958: 103)], holotype: A (2 sheets: A 00028320, 00028323[9], photos!); isotypes: BR (U00054979), F (V0092050F, photo!), GH (00028321, photo!; 00028322, photo!; 00028324, photo!), HAC (4535, fragment "X.3" inside envelop, photo!); K (000209135, photo!; 000209136, photo!; 000209137), NY (00071175, photo!; 00071178, photo!; 1662385, photo!; 1662390, photo!; 1662391, photo!), P (00725596, photo!; 00725597 photo!), US (00016510, photo!; 00989863, photo!)].

Etymology

The epithet honors Brother [Hermano] León (1871–1955, Fig. 4) from France, who was a member of the La Salle Catholic order. He was one of the most important botanists who between 1905 and his death in Havana studied the flora of Cuba (Alain 1956, Méndez Santos 2016).

[9] Protologue indicates that holotype is mounted in two sheets (Dahlgren and Glassman 1963: Figures 55–56).

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REFERENCES

Anonymous. 1896. Jahres-versammlung zu Wörlitz bei Dessau. Mitteilungen der Deutschen Dendrologischen Gesellschaft. 5: 1–2.

Anonymous. Sine die. Reseña Histórica de Portugalete, Cienfuegos, Cuba (available online at: https://www.monografias.com/trabajos66/historia-portugalete/historia-portugalete).

Alain H. 1956. Hermano León (1871–1955). Contribuciones Ocasionales del Museo de Historia Natural del Colegio "de la Salle." 15: 1–2.

Beccari O. 1907. Le palme Americane della tribu delle Corypheae. Webbia. 2: 1–343.

Beccari O. 1913. The palms indigenous to Cuba III. Pomona College Journal of Economic Botany. 3(1): 391–417.

Beccari O. 1931. Asiatic palms – Corypheae (revised and edited by U. Martelli). Annals of the Royal Botanic Garden, Calcutta. 13: 1–356.

Burkhardt L. 2016. Verzeichnis eponymischer Pflanzennamen. Index of Eponymic Plant Names. Index de Noms Eponymes des Genres Botaniques. Botanic Garden and Botanical Museum Berlin, Berlin.

Burret M. 1929. Palmae Cubenses et Domingenses a Cl. E.L. Ekman 1914–1928 lectae. Kungliga Svenska Vetenskaps-Akademiens Handlingar. Tredjen Serien. 6(7): 1–29.

Combs R. 1897. Some Cuban medical plants. Pharmaceutical Review. 15: 87–91, 109–112, 136.

Craft P. 2018. The Palms of Cuba. Palm Nut Pages, Inc., Sebastian, FL.

Dahlgren B. 1936. Index of American palms. Field Museum of Natural History Botanical Series. 14: 1–456.

Dahlgren B, Glassman S. 1958. A new species of *Copernicia* from Cuba. Principes. 2: 103–105.

Dahlgren B, Glassman S. 1963. A revision of the genus *Copernicia*. 2. West Indian species. Gentes Herbarum. 9(2): 43–232.

Denterghem OK. 1978. Les Palmiers. Histoire Iconographique. J. Rothschild, Paris.

Dowe JL. 2019. Wendland's palms. Hermann Wendland (1825–1903) of Herrenhausen Gardens, Hannover: his contribution to the taxonomy and horticulture of the palms (Arecaceae). Englera. 36: 1–137.

Dowe JL, Appelhans MS, Bräuchler C, Hilje L, Schlumpberger BO. 2022. The botanical expedition of Hermann Wendland in Central America: a nomenclatural study and travel report. Boissiera. 73: 1–136.

Dransfield J., Uhl NW, Asmussen CB, Baker WJ, Harley MM, Lewis CE. 2008. Genera Palmarum. The Evolution and Classification of Palms. Kew Publishing, Royal Botanic Gardens, Kew.

Glassman F. 1972. A revision of B. E. Dahlgren's index of American palms. Phanerogamarum Monographiae. 6: 1–294.

Greuter W, Brummitt RK, Farr ER, Kilian N, Kirk PM, Silva PC. 1993. NCU-3. Names in current use for extant plant genera. Regnum Vegetabile. 129: 1–1464.

Greuter W, Rankin Rodríguez R. 2022. Vascular Plants of Cuba. A Checklist. Third, Updated Edition of the Spermatophyta of Cuba. Botanic Garden and Botanical Museum Berlin, Berlin and Jardín Botánico Nacional, Havana.

Howard RA. 1988. Charles Wright in Cuba. 1856–1867. Chadwyck-Healey, Cambridge, United Kingdom.

Kitzke ED. 1962. Bror Eric Dahlgren. Principes. 6: 84–86.

Koster H. 1816. Travels in Brazil. Longman, London.

Lanjouw J, Stafleu FA. 1954. Index herbariorum. Part II. Collectors. Regnum Vegetabile. 2: 1–174.

Lapique Becali Z, Segundo Arias O. 2011. Cienfuegos. Trapiches, Ingenios y Centrales. Editorial de Ciencias Sociales, Havana.

León H. 1931. Contribución al estudio de las palmas de Cuba. Revista de la Sociedad Geográfica de Cuba. 4: 33–59.

León H. 1936. Contribución al estudio de las palmas de Cuba. Género *Copernicia* – II. Memorias de la Sociedad Cubana de Historia Natural "Felipe Poey." 10: 203–226.

Martelli U. 1921. Odoardo Beccari. Webbia. 5: 295–343.

Méndez Santos IE. 2016. El Hno. León (Joseph Silvestre Sauget) y sus aportes a la botánica cubana. Revista del Jardín Botánico Nacional. Universidad de la Habana. 37: 53–62.

Moya C. 2020. Charles Wright y las Palmas Cubanas. 6. Sauvalle "Flora Cubana". Repositorio de Información de Medio Ambiente de Cuba. Contribución al estudio de las palmas de Caribe (available online at: https://www.researchgate.net/publication/345740043_charles_wright_y_las_palmas_cubanas_6_sauvalle_flora_cubana_charles_wright_and_the_cuban_palms_6_sauvalle_flora_cubana).

Moya C. 2021a. An update of *Copernicia macroglossa* and *Copernicia ×escarzana* (Arecaceae). PalmArbor. 2021-07: 1–22.

Moya C. 2021b. Charles Wright in the Cuban flora 1. Citation of Sauvalle's *Flora Cubana*. PalmArbor. 2021-12: 1–22.

Moya C. 2023a. *Copernicia hospita* and *C. yarey* (Arecaceae): updated distribution for these Cuban endemics. PalmArbor. 2023-10: 1–23.

Moya C. 2023b. A further update on the nomenclature of *Copernicia glabrescens* and *C. macroglossa* (Arecaceae). PalmArbor. 2023-14: 1–9.

Moya C. 2025. Contributions of Brother León to the study of Cuban *Copernicia* (Arecaceae), 1931–1936. PalmArbor. 2025-04: 1–101.

Moya C, Terry M, Hernández Y. 2019. Novedades en la distribución conocida de *Copernicia ×escarzana* (Arecaceae); implicaciones para la conservación. Monteverdia. 12(2): 01–08.

Naranjo AA, Gandhi KN, Noblick L, Figueroa J, Francisco-Ortega J, Griffith MP. 2005. 1131. *Copernicia macroglossa* Schaedtler. Curtis's Botanical Magazine. 42: 3–17.

Noblick LR. 2009. Dr. Sidney Fredrick Glassman (1919–2008). Palms. 53: 153–155.

Pammel LH. 1899. Necrology: Arthur A. Crozier; Robert Combs; Carl Edward Schlabach. Proceedings of the Iowa Academy of Science. 7: 17–21.

Potztal E. 1959. Professor Dr. Max Burret 75 jahre alt. Willdenowia. 2: 140–142.

Puig-Samper MA, Naranjo Orovio C. 2016. Ramón de La Sagra, naturalista, geógrafo y cartógrafo de Cuba. Dvacáté století - The Twentieth Century. 8: 126–145.

Ramos JE. 1879. Elogio del académico Sr. D. Francisco A. Sauvalle. Anales de la Real Academia de Ciencias Médicas, Físicas y Naturales de La Habana. Revista Científica. 16: 38–52.

Regalado L, Ventosa I, Morejó R. 2008. Revisión histórica de los herbarios cubanos con énfasis en las series de especímenes. Revista del Jardín Botánico Nacional. Universidad de la Habana. 29: 101–138.

Reinke J. 1879. A. Grisebach. Botanische Zeitung. 37: 521–534.

Sauvalle FA. 1871. Flora cubana. Anales de la Real Academia de Ciencias Médicas, Físicas y Naturales de La Habana. Revista Científica. 7: 510–540, 560–566, 607–611, 715–717.

Sauvalle FA. 1873. Flora Cubana. La Antilla, Havana.

Schaedtler G. 1875. Die Palmen des Königl. Berggartens zu Herrenhausen bei Hannover. Hamburger Garten- und Blumenzeitung. 31: 20–27, 66–71, 110–115, 155–170, 213–221, 250–260.

Schaedtler G. 1895. Virginische kletterrose. Praktische Ratgeber im Obst und Gartenbau. 10: 208.

Secada Cárdenas E, Cárdenas González, CZ, Secada Cárdenas L, Escobar Blanco LM, Buides Secada L, Fernández Alfonso OM. 2015. Un acercamiento a la labor científica de Carlos de la Torre y Huerta. Revista Médica Electrónica. 37: 293–299.

Stearn WT. 1965. Grisebach's Flora of the British West Indian Islands: a biographical and bibliographical introduction. Journal of the Arnold Arboretum. 46: 243–285.

Trelles C. 1916. Biblioteca Científica Cubana. Volume 1. Imprenta de Juan F. Oliver, Matanzas, Cuba.

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A taxonomic revision of the "Quadrispina clade" of *Barleria* sect. *Prionitis*

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Abstract. The recently recognised Quadrispina clade within *Barleria* sect. *Prionitis* Nees (Acanthaceae) represents a taxonomically challenging group endemic to the Horn of Africa biodiversity hotspot. This study presents a comprehensive taxonomic revision of the complex, driven by morphological assessment and morphometric analyses. We recognise seven species in the complex in total, including four new species to science that had previously been included within *B. quadrispina*, namely *B. filtuensis, B. mudugensis*, *B. puberulifolia* and *B. sebsebei*. In addition, we recognise four subspecies within *B. quadrispina*, namely subsp. *quadrispina*, subsp. *glaucobracteata*, subsp. *waggana* and the newly described subsp. *kenyana*. Conservation assessments based on IUCN Red List categories and criteria indicate that *B. filtuensis, B. mudugensis, B. puberulifolia, B. sebsebei* and *B. quadrispina* subsp. *glaucobraceata* are range-restricted and potentially threatened by habitat degradation, hence they are preliminarily assessed as threatened under criterion B, whilst *B. quadrispina* subsp. *kenyana* remains Data Deficient.

Keywords: Ethiopia, extinction risk, hotspot, Kenya, phytogeography, Somalia, subsection, taxonomy.

INTRODUCTION

Barleria L. is the fourth largest genus of Acanthaceae, comprising approximately 300 species (Ensermu and Darbyshire 2018; Comito et al. 2022). Despite its remarkable diversity in macro- and micro-morphological characters and its high number of range-restricted species, it has only recently been the focus of concerted taxonomic and systematic research. Section *Prionitis* Nees is one of the most species-rich (and most consistently recognised) clades within *Barleria* with over 50 species. It is particularly rich in the drylands of Africa, with potentially the highest diversity in the Horn of Africa biodiversity hotspot (CEPF 2025). Species within this section are well-adapted to arid and semi-arid environments, often inhabiting open woodlands, thickets, and dry rocky slopes. A recent comprehensive RADseq phylogenetic analysis (Comito et al. 2022) has provided further resolution of relationships within *Barleria*, building on the earlier, predominantly plastid dataset of Darbyshire et al. (2019). Amongst several notable findings, Comito et al. (2022) highlighted the Quadrispina clade as a distinct group within sect. *Prionitis*, sister to the Core Prionitis clade. This Quadrispina clade is unique within sect. *Prionitis* in having corollas in the colour spectrum white to blue or mauve, whilst in the remainder of sect. *Prionitis* the corollas are in the spectrum white to yellow, orange, ochre-coloured or red. Therefore, the *Quadrispina* clade is now in the process of being formally recognised as a distinct subsection, subsect. *Cyanoprionitis* I.Darbysh. & Comito, as part of a global infrageneric reclassification of *Barleria* (Darbyshire and Comito, in press).

Species delimitation within the Quadrispina clade is challenging, in particular how to delimit the widespread species *Barleria quadrispina* Lindau and closely allied localised taxa or variants (Ensermu 2006; Hedrén 2006a; Darbyshire et al. 2010). Previous taxonomic efforts have resulted in the recognition of three species within the clade, including *B. ferox* Ensermu & I.Darbysh. and *B. negeleensis* Ensermu & I.Darbysh. as two range-restricted species endemic to Ethiopia (Ensermu and Darbyshire 2018), following their earlier informal recognition as undescribed species in the *Flora of Ethiopia and Eritrea* (Ensermu 2006). Elsewhere, Hedrén (2006b) proposed *B. glaucobracteata* Hedrén as a distinct species from southwest Somalia, although he did not recognise this species to be allied to the *B. quadrispina* complex, instead comparing it to the yellow-flowered *B. linearifolia* Rendle, nor did he note that the same taxon occurs in neighboring regions of Ethiopia and Kenya. Later, *B. glaucobracteata* was synonymised within a broadly circumscribed *B. quadrispina* Lindau by Darbyshire et al. (2010). In addition, other potentially distinct species from Somalia were listed only as 'notes' under *B. quadrispina* by Hedrén (2006a), remaining undescribed.

The aims of the current study are therefore to reassess the taxonomy and species delimitation within the Quadrispina clade (subsect. *Cyanoprionitis*) and to describe any arising new taxa to science. Morphometric analysis is used to help visualize morphological variation in the complex and inform species delimitation. Together with the recently described *B. biramosa* Defty & I.Darbysh., *B. compacta* Malombe & I.Darbysh. subsp. *minima* I.Darbysh. & Defty and *B. praetermissa* I.Darbysh. (Defty and Darbyshire 2024; Hanny et al. 2024), the present revision adds to ongoing taxonomic work that highlights the high diversity of *Barleria* sect. *Prionitis* and the rich endemic Acanthaceae flora of the Horn of Africa biodiversity hotspot.

MATERIALS & METHODS

Herbarium specimens of the potential new taxa and morphologically allied species housed at B, C, EA, ETH, FT, K, MO, P, PRE and UPS herbaria were analysed and measured, using standard herbarium practices; herbarium abbreviations follow Thiers (updated continuously). Prior to dissection, flowers were soaked in Aerosol OT 5% solution; all other characters were measured on dry material. All duplicates seen by at least one of the authors are marked with "!"; those only seen as electronic images are marked "*". Barcodes for duplicates are listed wherever available to facilitate digital access to the specimens.

Morphometric trait data, where possible, were recorded for all examined specimens, including: stem width; stem, leaf and inflorescence indumentum; longest spine ray length; leaf, bract and bracteole shape, size and length: width ratio; and presence of broad sessile glands on the bracts and bracteoles. Measurements were taken using a ruler or Leica S9E microscope with a 0.1 mm scale graticule. Where possible for each quantitative character, an average value per specimen was calculated from up to 10 measurements per specimen. A principal component analysis (PCA) was conducted in R version 4.1.2 (R Core Team 2021) using the *prcomp* function of the built-in *stats* package (version 3.6.2), with the dataset imported as a matrix. Due to the requirement of the PCA for quantitative traits, only the following characters could be used in the final analysis: leaf length: width ratio, bract length: width ratio, bracteole length: width ratio, and maximum corolla length. As such, diagnostic characteristics for some taxa are not included in the PCA.

Description of the range of each species includes reference to the relevant floristic regions from the *Flora of Ethiopia and Eritrea*, the *Flora of Somalia* and the *Flora of Tropical East Africa*. For Ethiopia, we use the two-letter codes that relate to the provinces during the time of Emperor Haile Selassie, namely AF = Afar, BA = Bale, GG = Gamo Gofa, HA = Harerge, SD = Sidamo, SU = Shewa and TU = Tigray (see Hedberg et al. 2009). For Somalia, we use the eight geographic regions of the Flora, three in the north (N1, N2, N3), two in the central region (C1, C2) and three in the south (S1, S2, S3; see Thulin 1993). For Ethiopia, we use the seven subdivisions of Kenya, the only one of relevance being K1 (see Polhill 1988). The distribution maps for the relevant taxa were produced in ArcGIS Pro v.3.5, using georeferenced herbarium collections. The species conservation (extinction risk) assessment follows the Categories and Criteria of the IUCN Red List (IUCN 2012) and the guidelines for their use (IUCN 2024). Extent of Occurrence (EOO) and Area of Occupancy (AOO) were calculated using the GeoCAT tool (https://geocat.iucnredlist.org/; Bachman et al. 2011).

RESULTS

Our detailed morphological investigation of the Quadrispina clade in *Barleria* sect. *Prionitis* is based upon 143 specimens of which 82 were studied directly by the first and last authors and the remaining 61 were studied remotely via digital images or in-person by the other authors. This research reveals that several distinct taxa are readily recognizable based on variation in a suite of characters, with type(s) and density of vegetative and inflorescence indumentum; leaf dimensions and shape; inflorescence form; bract, bracteole and calyx colour and shape; and corolla colour and size all being significant in differentiating the taxa.

A total of seven species are recognised within the Quadrispina clade based on morphological and distributional data. These include four newly described species – *Barleria filtuensis* Defty & I.Darbysh., *B. mudugensis* Defty & I.Darbysh., *B. puberulifolia* Defty & I.Darbysh., and *B. sebsebei* Defty & I.Darbysh. – in addition to the previously described *B. ferox, B. negeleensis* and the widespread *B. quadrispina*. The lattermost species is further subdivided into four subspecies, including one newly described taxon – *B. quadrispina* subsp. *kenyana* Defty & I.Darbysh. – and two newly assigned combinations for taxa previously treated as separate species before subsequently being included within *B. quadrispina* s.l. – *B. quadrispina* subsp. *glaucobracteata* (Hedrén) Defty & I.Darbysh. and *B. quadrispina* subsp. *waggana* (Rendle) Defty & I.Darbysh. – to reflect the significant infraspecific morphological and geographical differentiation within *B. quadrispina*.

Principal Component Analysis

The purpose of the PCA was to visualise morphological variation in the Quadrispina clade to help inform species delimitation. The analysis was limited to four measurable traits and thus captures only a subset of the morphological variation present. Other taxonomically important characters, such as indumentum, flower colour and the presence and density of broad sessile glands on the bracts and bracteoles, could not be included in the PCA due to their qualitative nature. Similarly, only specimens which had measurable aspects for all characteristics could be included within the PCA. Hence, some taxa are only represented by a single specimen within the PCA, often due to the absence of measurable corollas. As such, of the 82 specimens studied directly by the first author in the Quadrispina clade, 64 were used for the PCA analysis (Table S1). The PCA of the vegetative (leaf, bract and bracteole l:w ratio) and floral (maximum corolla length) traits revealed that the first two principal components accounted for approximately 64.1% of the total variance. PC1 was primarily associated with bract and bracteole length: width ratios, which both loaded strongly and positively (0.64 and 0.65), while PC2 was driven largely by corolla length, which loaded negatively (-0.84), and leaf length: width ratio (-0.54). The results of the PCA can be further explored in Figure 1.

The taxon here described as *Barleria filtuensis* shows considerable separation from the other taxa, likely on account of its high leaf length: width ratio. Similarly, *B. negeleensis* appears distinct in its separation from the taxa identified in this account. *Barleria ferox* and *B. sebsebei*, the latter newly described here, form distinct clusters in the PCA, although there is some degree of overlap between them. However, these taxa can be reliably distinguished when characters in the PCA are combined with other morphological traits such as leaf shape, spine length and calyx indumentum. Clustering can also be observed between the different forms of *B. quadrispina* that are here described as subspecies, supporting the taxonomic grouping of these taxa. Overlap between these groupings may be attributed to the absence of traits such as indumentum type and bract/bracteole colour in the PCA – important characteristics in delimiting these subspecies. Notably, *B. quadrispina* subsp. *waggana* differentiates itself from subsp. *quadrispina* with its dense indumentum of bulbous-based hairs. *Barleria quadrispina* subsp. *glaucobracteata* and subsp. *kenyana* are separated from subsp. *quadrispina* and subsp. *waggana* due to their notably larger leaves and higher leaf length: width ratios. However, these two taxa show some clumping because much of their distinction is characterised by indumentum and bract/bracteole colour. It is important to note that *B. mudugensis* and *B. puberulifolia*, both newly described here, were both represented by only one specimen in the analysis. *Barleria mudugensis* is the only taxon with biramous hairs, an unusual characteristic

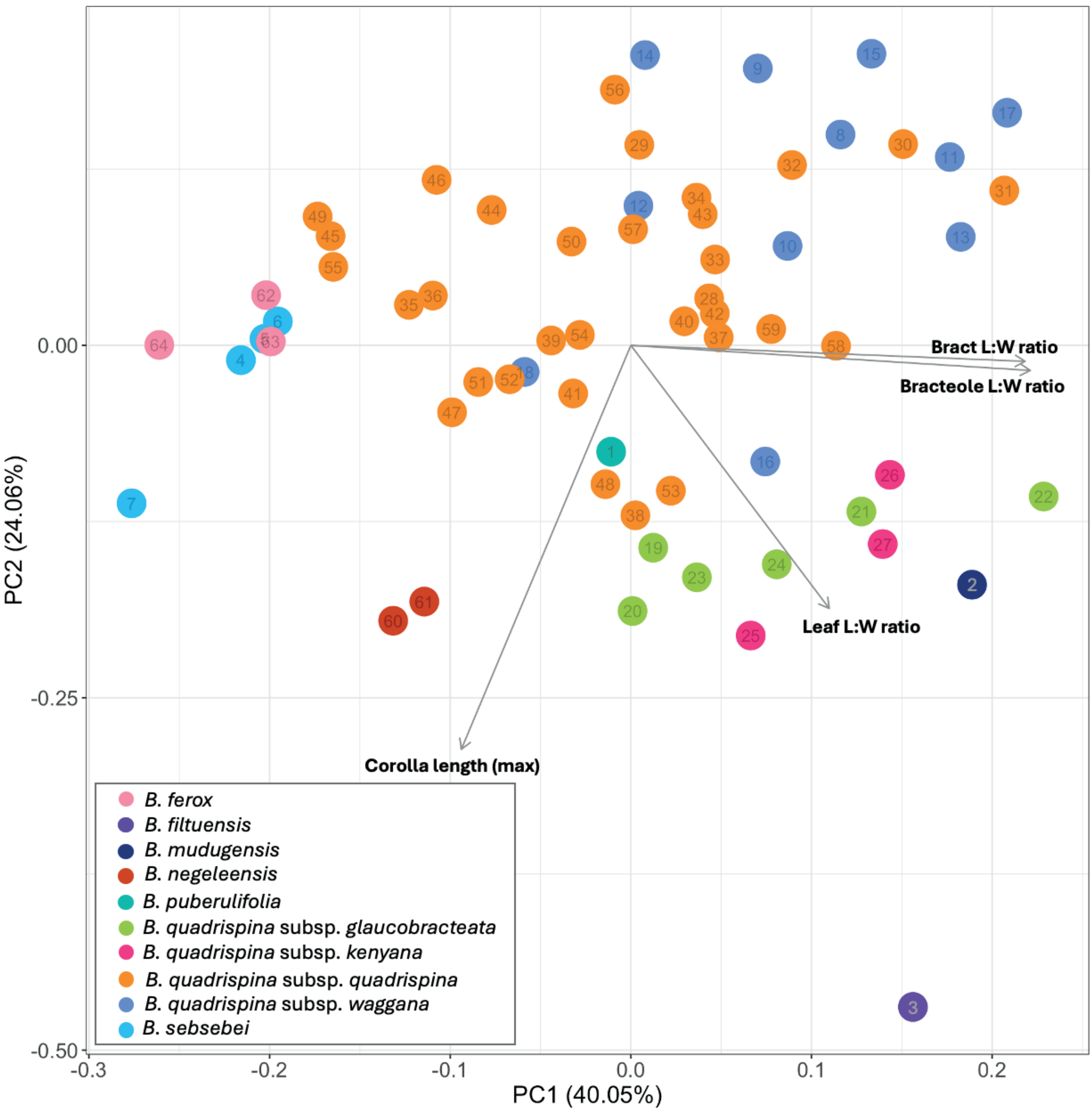

Figure 1. Principal Components Analysis (PCA) of morphological traits across taxa of *Barleria* in the Quadrispina clade.

within *Barleria* sect. *Prionitis*. It is also characterised by the dense, broad sessile glands present at the base of the bracts and bracteoles – not captured by this PCA. *Barleria mudugensis* is also geographically disjunct from its closest clustering taxa in the PCA, namely *B. quadrispina* subsp. *glaucobracteata* and subsp. *kenyana,* occurring in the Mudug Region of north-central Somalia. Similarly, despite *B. puberulifolia* clustering within *B. quadrispina,* this species separates itself geographically, located in northern Somalia, and is characterised by its leaf, bract, bracteole and calyx indumentum.

Extinction risk

Preliminary conservation assessments suggest that several taxa within the Quadrispina clade face elevated extinction risk and are likely to qualify as threatened on the IUCN Red List due to habitat degradation within their restricted geographic ranges. Specifically, the newly described species *B. filtuensis, B. mudugensis, B. puberulifolia* and *B. sebsebei* provisionally qualify as threatened alongside *B. quadrispina* subsp. *glaucobracteata*, whilst the newly described *B. quadrispina* subsp. *kenyana* is considered to be Data Deficient. The previously described *B. ferox* and *B. negeleensis* are also currently assessed as Endangered on the Red List (Darbyshire and Roberts 2023; Darbyshire et al. 2023). Within *B. quadrispina,* subsp. *quadrispina* and subsp. *waggana* are considered to be of Least Concern.

TAXONOMIC ACCOUNT

Key to species and subspecies in the *Barleria quadrispina* Clade

1. Cream-coloured biramous hairs present on the stems, leaves and bracts; each unit (axil) of the flowering spike single-flowered..**1. *B. mudugensis***

   Cream-coloured biramous hairs absent, all hairs unbranched; each unit (axil) of the flowering spike 3–7-flowered, at least when mature (distal axils can be single-flowered) **2**

2. Calyx with a dense mixed indumentum of glandular and eglandular hairs covering the external surface; the entire inflorescence usually densely and conspicuously hairy (can be less so at fruiting) **3**

   Calyx glabrous or sparsely hairy with no or few glandular hairs, or if with a mixed indumentum of glandular and eglandular hairs then less dense, the surface still visible, the inflorescence not so densely and conspicuously hairy (except in *B. quadrispina* subsp. *waggana* where glandular hairs are absent) **5**

3. External surface of corolla puberulous; leaves puberulent with minute (sub-) appressed white hairs, venation inconspicuous, 2 (–3) lateral veins per side, leaf blade lanceolate to obovate or ovate-elliptic, 23–28 × 6.2–11 mm, length: width ratio 2.5–3.7: 1...............................**4. *B. puberulifolia***

   External surface of corolla glabrous; leaves pubescent with bristly hairs at least along margin, these sometimes also numerous on the midrib and veins abaxially, with conspicuous venation, 3–5 lateral veins per side, linear-lanceolate to narrowly oblong-elliptic, leaf length >50 mm, length: width ratio 3.7–11: 1...**4**

4. Leaves linear-lanceolate to -oblanceolate, length: width ratio 8.3–11: 1; bracteoles and calyces with long ascending bristly eglandular hairs 1–1.7 mm long and shorter patent, non-glossy glandular hairs 0.4–0.6 mm long; bracts towards base of spike 24–24.5 × 3–6 mm including spine tip 1.5–4 mm long, bracts becoming linear-lanceolate distally..**2. *B. filtuensis***

   Leaves narrowly oblong to oblong-elliptic, leaf length: width ratio 3.7–5.2: 1; bracteoles and calyces with ascending bristly eglandular hairs 0.3–0.5 mm long and longer patent, glossy glandular hairs 0.4–1.2 mm long; bracts towards base of spike 22–40 × 8.5–17 mm including prominent grey apical spine 4–8 mm long, bracts becoming oblanceolate distally .... **3. *B. negeleensis***

5. Broad sessile glands numerous and conspicuous at base of bracts and bracteoles **6**

   Broad sessile glands absent or sparse and inconspicuous on the bracts and bracteoles (5. *B. quadrispina*)................**7**

6. Axillary spines rather slender, sessile or stalk to 2 mm long, with ascending rays 17–22 (–29) mm long; leaves broadly elliptic to suborbicular or occasionally ovate, 22–39 mm wide, length: width ratio 1.2–1.7: 1, surfaces pubescent in addition to long bristly hairs along midrib and veins beneath and margins; anterior and posterior calyx lobes lanceolate, more gradually narrowed into long apical seta, ± 8.5–9.5 mm long at flowering including seta. ....**6. *B. sebsebei***

   Axillary spines very stout, stalked for (4–) 8–16 mm, with widely divergent rays typically 22–32 mm long; leaves oblong-elliptic or -obovate, 13–25 mm wide, length: width ratio 1.9–2.1: 1, sparsely strigulose along midrib adaxially, main veins abaxially and margin; anterior and posterior calyx lobes broadly ovate, abruptly narrowed into short apical seta, 4.2–5.5 mm long at flowering including seta ....**7. *B. ferox***

7. Bract length: width ratio at midpoint of inflorescence 9.6–10: 1; calyx with long glandular hairs and fine short patent eglandular hairs on external surface....................................... ....**5d. *B. quadrispina*** subsp. ***kenyana***

   Bract length: width ratio at midpoint of inflorescence 3.7–9: 1; calyx glabrous or eglandular hairs present along margins (these sometimes bulbous based) and/or sometimes with few glandular hairs on external surface.......................**8**

8. Bracts and bracteoles green, densely and conspicuously hairy, always with bulbous-based hairs numerous along the margins, glandular hairs absent; leaves usually obovate, more rarely oblanceolate, length: width ratio 2–2.7 (–3.7): 1, corollas blue or purple...**5b. *B. quadrispina*** subsp. ***waggana***

   Bracts and bracteoles if with bulbous-based hairs numerous along the margins, then less densely and conspicuously hairy and glandular hairs also present on the surface; leaves variously oblanceolate, oblong-elliptic or more rarely obovate, length: width ratio 3.2–6.5: 1, corollas white, blue or purple **9**

9. Bracts and bracteoles green or at most slightly glaucous; corolla white, blue or purple, 16–30 mm long ....**5a. *B. quadrispina*** subsp. ***quadrispina***

Bracts and bracteoles conspicuously pale glaucous to white; corolla always white, 28–34 mm long.. **5c. *B. quadrispina*** subsp. ***glaucobracteata***

1. *Barleria mudugensis* Defty & I.Darbysh., **sp. nov.**

Type: Somalia, 23 km S of Jeriban, 07°01'N, 48°52'E, 27 May 1979 (fl.), *J. B. Gillett, C. F. Hemming & R. M. Watson 22097* (holotype K! [K001295239]; isotype EA! [EA000043822]). Figure 2.

Diagnosis

Barleria mudugensis has previously been confused with *Barleria quadrispina* but differs in (1) the stem being densely covered in cream-coloured biramous hairs (versus largely glabrous to pubescent with many short spreading white unbranched hairs); (2) the leaf indumentum being strigose with unequally and equally biramous hairs (versus strigose with unbranched hairs); (3) the cymes at each axil of the inflorescence being 1-flowered (versus 3–7-flowered); (4) the bracts strigose with appressed hairs, which are mixed unbranched and biramous (versus appressed to spreading unbranched hairs with or without a bulbous base and surface sometimes with patent glandular hairs); (5) the abaxial bract surface having numerous and conspicuous broad sessile glands (versus broad sessile glands absent or very few abaxially); and (6) the external surface of the calyx having unbranched and biramous strigose hairs, with short glandular hairs occasionally along the margin (versus glabrous to densely eglandular and/or glandular unbranched hairs, with or without coarse bulbous-based hairs along the margin). Table 1.

Description

Harshly spiny compact shrublet, 10–15 cm tall; young stems 4-angular, densely covered in cream-coloured appressed biramous hairs throughout, giving the stems a pale-glaucous appearance; mature stems turning woody, 3–4 mm in diameter, sometimes with numerous scars at the nodes between short internodes. *Axillary spines* numerous, beige-white, subsessile or stalk to 2.5 mm long, 4-rayed, rays of similar length, ± straight, longest rays 22–26 mm long, eglandular hairs present at base of spines. *Leaves* on short and ill-defined petioles 2–3 mm long, pubescent with short fine hairs; blade (oblong-) obovate, 27–30 × 9–11 mm (length: width ratio 2.7–3: 1), base attenuate, margin entire, apex acute to obtuse with apical spine 1.2–2.1 mm long, adaxial surface sparsely strigose but more densely strigose along midrib, abaxial surface at first densely strigose, more sparse at maturity when most dense along midrib, hairs cream-coloured, equally and unequally biramous, 0.3–0.6 mm long, also with few broad sessile glands towards the base abaxially; lateral veins 2–3 per side, strongly ascending, inconspicuous. *Inflorescences* terminal, spiciform, 2–4.5 cm long, each axil single-flowered, flowers sessile; bracts at base of inflorescence green, elliptic-obovate, 12.3–14.5 × 4.3–4.8 mm, apex tapered into spine tip 2.7–4 mm long, gradually becoming paler grey-green and narrowing up the spike, becoming linear–lanceolate distally where 18–24 × 1.6–1.8 mm including long-spinose apex; abaxial surface strigose, most dense on midrib, with both unbranched and biramous hairs present, and with numerous, conspicuous broad sessile glands most dense proximally towards midrib, adaxial surface as abaxial, but without broad sessile glands; bracteoles greenish-white, linear-lanceolate, spinose, 16–21 × 1–1.5 mm mm, with few appressed unbranched and biramous hairs along midrib towards base abaxially, and with broad sessile glands towards base. *Calyx* pale grey-green, eventually turning white; anterior and posterior lobes subequal, with base broadly elliptic-orbicular and with abrupt long-cuspidate apex, 8–9.8 × 2–2.8 mm including spine tip 4–4.7 mm long, midrib somewhat prominent, external surface strigose, hairs concentrated proximally, both unbranched and biramous hairs present, also with short glandular hairs present along margin, internal surface shortly pubescent; lateral lobes narrower, ± 8.8 × 1.8 mm, apex attenuate. *Corolla* white or white becoming lilac, 30–35 mm long, glabrous externally; tube cylindrical, 14–18 mm long, ± 2.5 mm diameter; limb in weak "4+1" configuration; abaxial lobe offset by ± 3.8 mm, obovate, ca. 19 × 9.5 mm, apex rounded, lateral lobes broadly elliptic to obovate, 16.6–17.4 × 9.6–9.8 mm, apices obtuse (ratio of abaxial: lateral lobe length ± 1.1: 1); adaxial lobes oblanceolate, ± 17.2 × 7.2 mm, apices obtuse. *Stamens* inserted 5.3–5.5 mm from base of corolla tube; filaments of long stamens 16.5–17 mm long, shortly and sparsely hairy at base, elsewhere glabrous; anthers ± 2.6 mm long; short lateral stamens with filaments 1.6–1.7 mm long, sparsely pubescent at base, antherodes 0.8–0.9 mm long. *Ovary* glabrous; style ± 35 mm long, glabrous; stigma linear, 0.5–0.9 mm long. *Capsule* and seeds not seen.

Etymology

Barleria mudugensis is named after the Mudug Region of Somalia, to which it is endemic.

Distribution

Occurs only in Hobyo and Jeriban Districts, Mudug Region of north-central Somalia (C1 floristic region). Fig. 3.

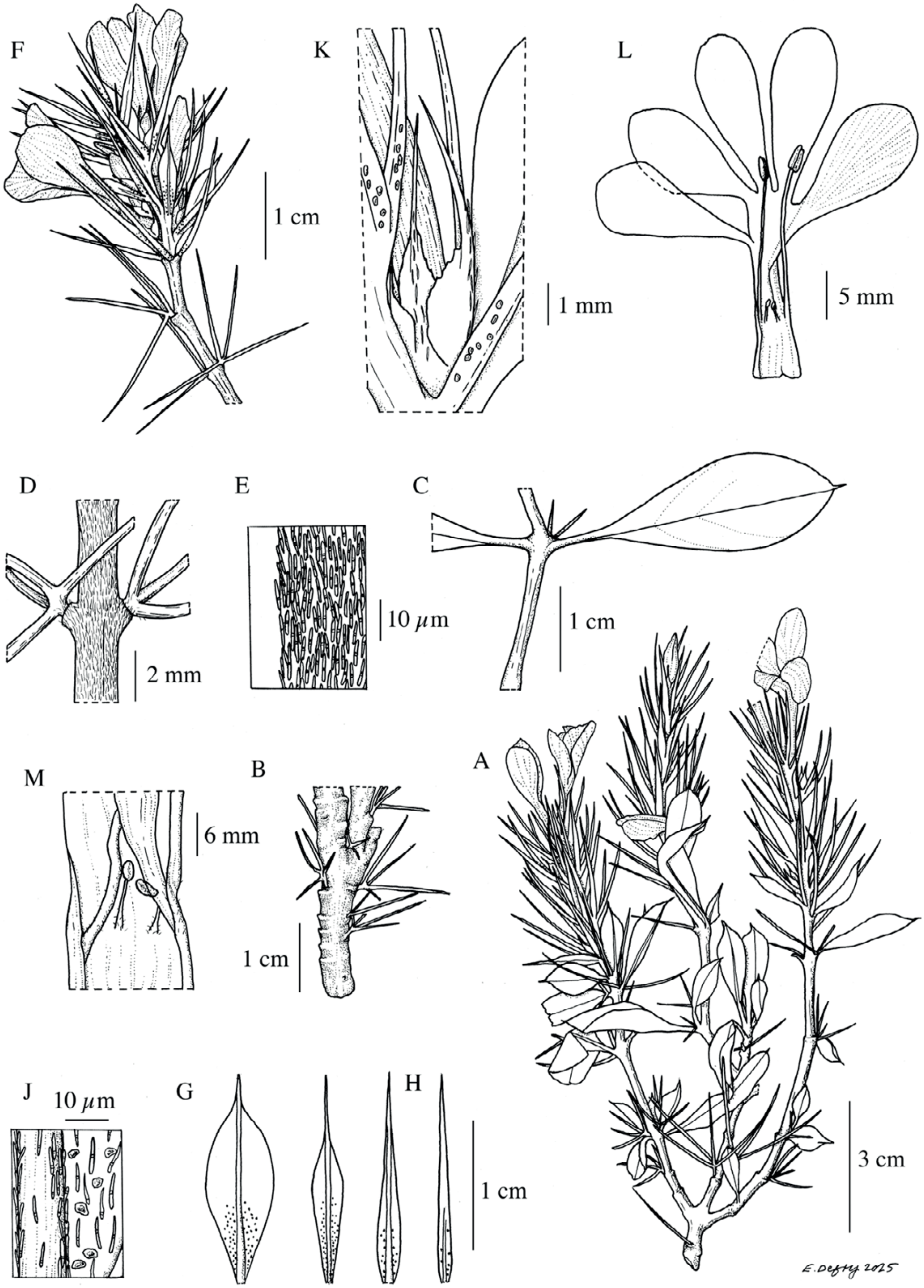

Figure 2. *Barleria mudugensis*. **A.** Habit, flowering branch. **B.** Mature stem, with axillary spines. **C.** Leaf in situ, abaxial surface, with axillary spines. **D.** Young stem, with indumentum and axillary spines. **E.** Detail of young stem indumentum. **F.** Inflorescence, flowering, with axillary spines. **G.** Bracts, variation in shape from proximal (l) to distal (r) bracts. **H.** Bracteole. **J.** Leaf indumentum, with biramous hairs and broad sessile glands. **K.** Flowering calyx, with base of bracts and bracteoles. **L.** Dissected corolla with androecium, abaxial corolla lobe to the left. **M.** Short lateral stamens. A, C–M. from *J. B. Gillett et al. 22097* (K, holotype)*;* B. from *R. G. Wieland 4567* (K). Drawn by Ellie Defty.

Habitat and Ecology

This species is known to occur at ca. 150 m asl. The vegetation in the area is open deciduous bushland on shallow soil or sand overlying limestone. Examples of other narrow endemics with similar distributions are *Endostemon stenocaulis* (Hedge) Ryding, A.J.Paton & Thulin, *Oxygonum thulinianum* S.Ortiz and *Zygocarpum gillettii* (Thulin) Thulin & Lavin.

Conservation status

With only two known localities and an area of occupancy (AOO) of 8 km^2, this is a highly range-restricted species, although it was noted to be locally common by J. B. Gillett *et al.* (22097). Whilst specific habitat information is unknown, this species has been collected from the Hobyo grassland and shrubland ecoregion. Although the area is sparsely populated, overgrazing and wood collecting are general threats to the habitat of this region. In addition, the collection by R. G. Wieland (4567) was collected near the roadside, suggesting potential vulnerability to habitat disturbance from road improvement. The two known localities are considered to be separate locations and, with the threats noted above, this species is considered likely to qualify as **Endangered** under criteria B: **EN B2ab(iii)**.

Taxonomic notes

Hedrén (2006a) noted that the type specimen of this species is similar to his *Barleria glaucobracteata* (= *B. quadrispina* subsp. *glaucobracteata* in the current treatment) but that it differs in having shorter leaves, the bracts and bracteoles having few bristle-like hairs and densely dotted with sessile glands on the lower surface towards the base, and broader calyx lobes with a more distinctly delineated spine distally. He had earlier (2004) annotated the specimen as a possible sp. nov. near *B. quadrispina*, differing in having a silvery indumentum of appressed hairs on the stem. Hedrén did not note that these silvery hairs are biramous, this being the only species within the *Barleria quadrispina* to have such an indumentum. This, together with the conspicuous and numerous sessile glands on the bracts, plus the fact that each unit of the spiciform inflorescence is single-flowered, allows this species to be readily separated from *B. quadrispina*.

Additional specimens examined

SOMALIA. Hobyo Region: W of Labawarood, Stand 153, 06°26'30"N, 48°35'12"E, 20 June 1987 (fl.), *R. G. Wieland 4567* (K! [K001295252], MO).

Table 1. A comparison of the diagnostic characters for separation of *Barleria mudugensis* and *B. sebsebei* from *B. quadrispina.*

Character	*B. mudugensis*	*B. quadrispina*	*B. sebsebei*
Stem indumentum	Densely covered in cream-coloured appressed biramous hairs	Largely glabrous or with many short spreading white hairs	Sparsely pubescent with short bristly unbranched hairs
Leaf indumentum (abaxial surface)	Strigose, hairs equally and unequally biramous	Strigose at least on the margin, hairs unbranched	Short fine ascending hairs, most dense along veins, hairs unbranched, margins and occasionally midrib strigose
Leaf length: width ratio	2.7–3: 1	2–6.5: 1	1.2–1.7: 1
Leaf width	9–11 mm	8–24 mm	22–39 mm
Cyme at each axil of inflorescence when mature	1-flowered	3–7-flowered	3–7-flowered
Bract indumentum (adaxial surface)	Strigose, unbranched and biramous hairs present	Margin and midrib with coarse appressed to spreading hairs with or without a bulbous base, surface sometimes also with patent glandular hairs, hairs unbranched	Glabrous or sometimes with short fine hairs along midrib and veins, hairs unbranched
Glands on bracts (abaxial surface)	Numerous, conspicuous broad sessile glands	Broad sessile glands occasional or absent	Conspicuous and ± numerous broad sessile glands
Calyx indumentum (external surface)	Both unbranched and biramous hairs present, also with short glandular hairs present along margin	Surface glabrous to eglandular- and/or glandular-pubescent, with or without coarse, ± bulbous-based hairs along margin	Glabrous or with short ascending or appressed eglandular hairs concentrated proximally along midrib
Corolla length	30–35 mm	17–34 mm	30–37 mm

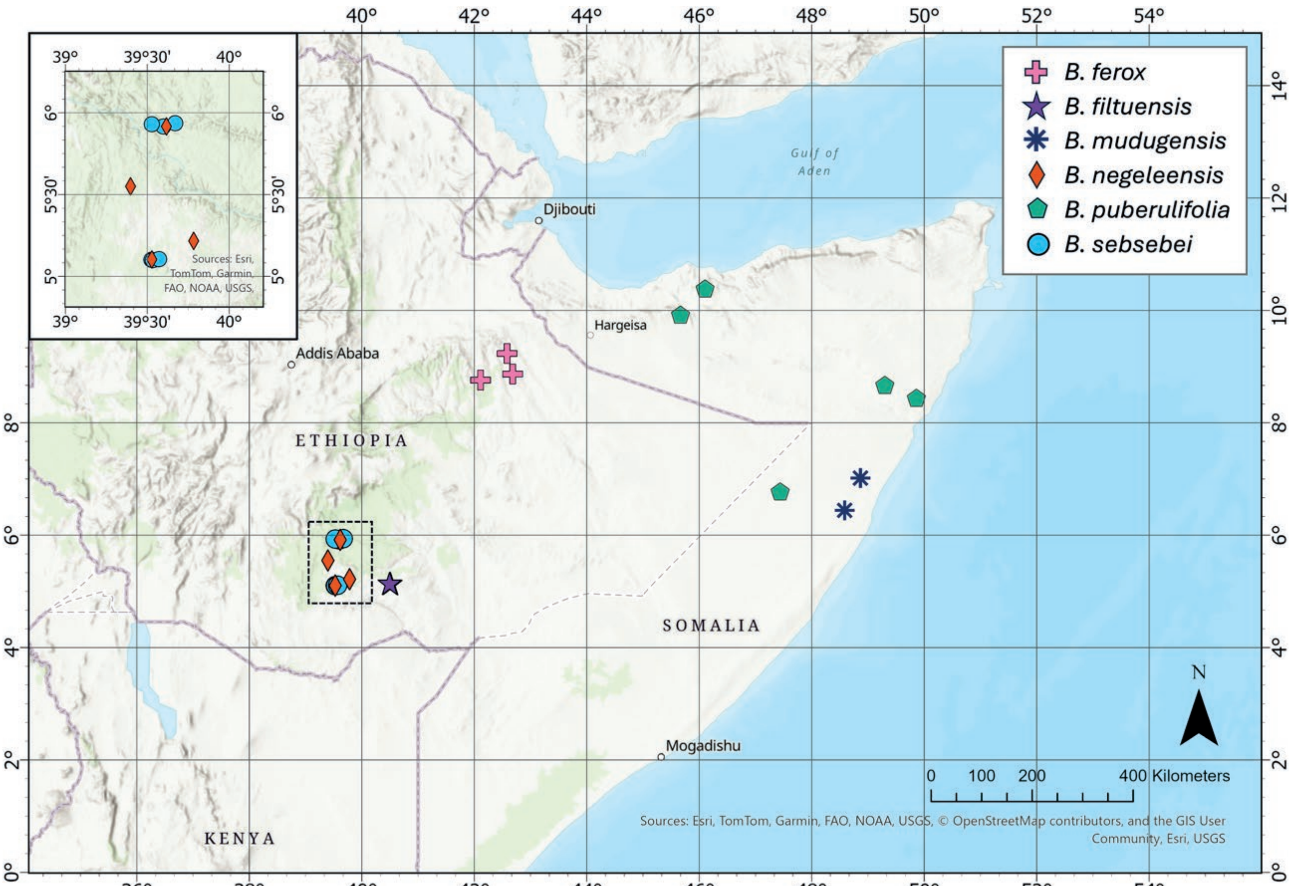

Figure 3. Geographic distribution of four newly described *Barleria* species within the Quadrispina clade, *B. filtuensis, B. mudugensis, B. puberulifolia* and *B. sebsebei,* and two closely allied species, *B. ferox and B. negeleensis,* from northeastern Africa. Zoomed inset (indicated by dashed box) clarifies the overlapping ranges of *B. negeleensis* and *B. sebsebei.*

2. ***Barleria filtuensis*** Defty & I.Darbysh., **sp. nov.**

Type: Ethiopia, Sidamo, Filtu to Negelle, 17 km from Filtu, 05°08.5'N, 40°30.5'E, 8 Dec. 2012 (fl.), *I. Friis, Sebsebe D., Wege A. & Ermias G. 14839* (holotype K! [K001295211]; isotypes C, ETH); Figure 4.

Diagnosis

Barleria filtuensis is most likely to be confused with *B. negeleensis* but differs in (1) the basal stem width being 1.5–3.6 mm (versus 5–8 mm); (2) the leaf length: width ratio being 8.3–11: 1 (versus 3.7–5.2: 1); (3) the bracteole and calyx indumentum comprising long-ascending bristly, glossy eglandular hairs 1–1.7 mm long and shorter patent, non-glossy glandular hairs 0.4–0.6 mm long (versus densely pubescent with ascending bristly eglandular hairs 0.3–0.5 mm and longer patent, glossy glandular hairs 0.4–1.2 mm); (4) the anterior calyx lobes being ± 16.8 × 3.5 mm including spine tip 6 mm long, with no visible midrib or lateral veins (versus (11–) 14–17 × 4–6 mm including spine tip 2.5 mm long, with prominent midrib and lateral veins); (5) the bracts towards the base of the spike (but excluding basal pairs) being lanceolate to linear-lanceolate, 24–24.5 × 3–6 mm including apical spine 1.5–4 mm (versus bracts towards base of spike ovate to oblong-elliptic, 22–40 × 8.5–17 mm including prominent grey apical spine 4–8 mm long). Table 2.

Description

Spiny slender shrublet, 8.5–16 cm tall; young stems green, 4-angular, pubescent with long ascending bristly hairs, increasing in density at and immediately below nodes, most dense on two opposite sides; older stems woody, 1.5–3.6 mm in diameter. *Axillary spines* beige-white, stalk 1.5–5.9 mm long, 4-rayed, rays of similar length or 2 longer, straight, longest ray 16–17.5 mm long; occasional 2-rayed spines present in the distal leaf axils

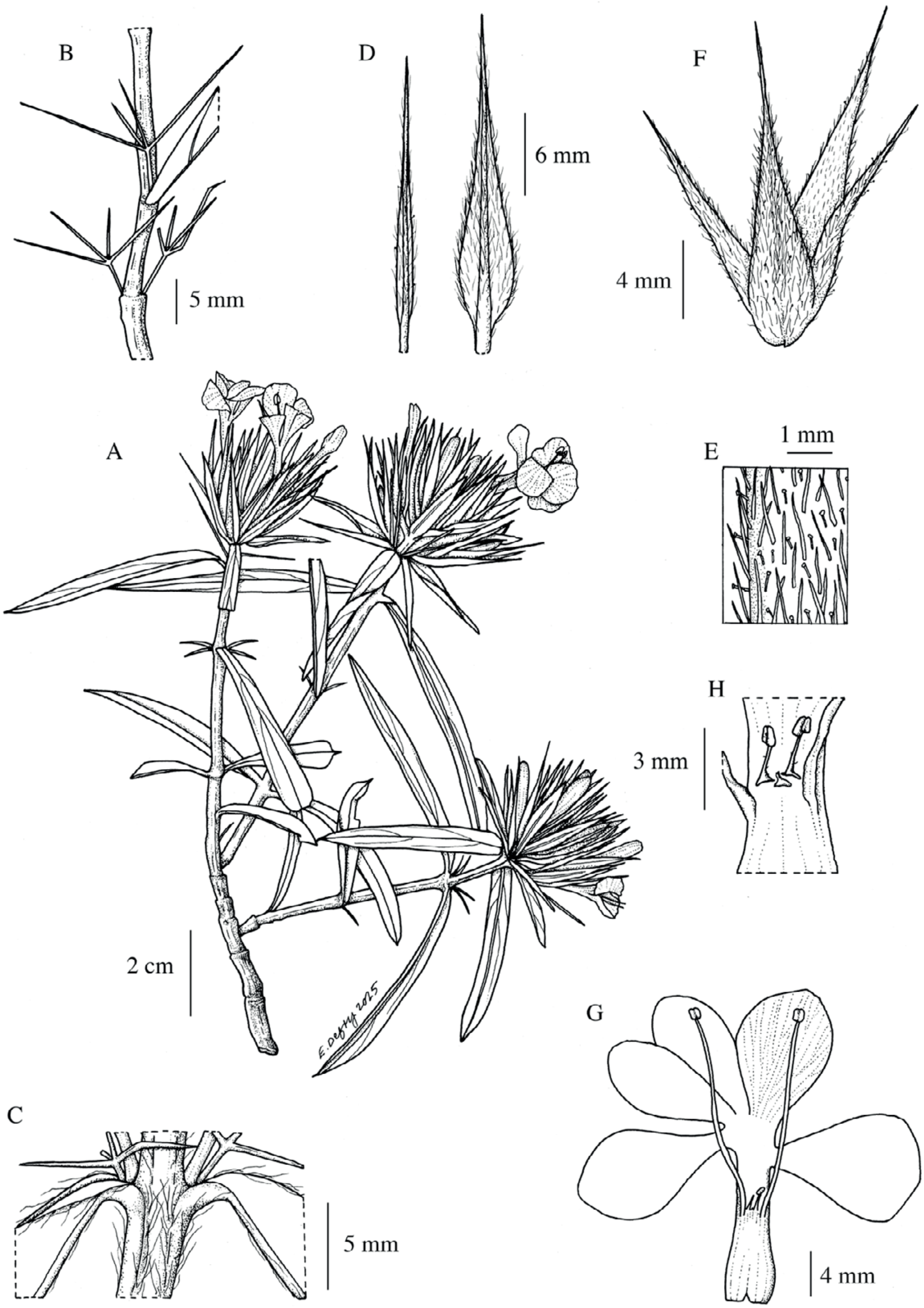

Figure 4. *Barleria filtuensis.* **A.** Habit, flowering branch. **B** Young stem, with axillary spines, including broken spines. **C.** Young stem at node, with indumentum and axillary spines. **D.** Bracteole (l) and bract (r), abaxial surfaces. **E.** Detail of bract indumentum. **F.** Calyx, with indumentum. **G.** Dissected corolla with androecium, abaxial corolla lobe to the right. **H.** Short lateral stamens and staminode. A–H. from *I. Friis et al. 14839* (K, holotype). Drawn by Ellie Defty.

resembling bracteoles, sessile; occasional compound spines present in the distal axils that are many branched. *Leaves* subsessile; blade linear-lanceolate to -oblanceolate, 55–69 × 5–8 mm (length: width ratio 8.3–11: 1), base cuneate, margin entire, apex acute, sometimes with a minute apical spine 0.5–0.7 mm long, adaxial surface often glabrous, abaxial surface with long somewhat bristly ascending hairs 1.4–2.1 mm long, most dense along midrib and margin, hairs unbranched, 1–2.6 mm long; lateral veins 3–4 per side, strongly ascending, prominent abaxially, midrib prominent abaxially and adaxially. *Inflorescences* terminal, subcapitate or shortly and densely spiciform, 2.5–4 cm long, each axil with a 3–7-flowered dichasial cyme; basal bracts leaf like, bracts towards centre of spike green, lanceolate, 24–24.5 × 3–6 mm including spine tip 1.5–4 mm long, gradually becoming more linear-lanceolate distally, abaxial surface and margin with dense long ascending, bristly eglandular hairs, glabrous adaxially; bracteoles green-white, linear-lanceolate, spinose, 19–20 × 1.1–1.5 mm, with ascending eglandular bristly hairs 1–1.7 mm long and patent glandular hairs 0.4–0.6 mm long on both surfaces and margins; flowers shortly pedicellate, pedicel fused to the subtending bracteole. *Calyx* green; anterior lobe lanceolate, ± 16.8 × 3.5 mm including spine tip (one calyx measured), apex with grey spine 6 mm long; external surface densely eglandular-pubescent with long ascending bristly hairs, and with numerous shorter glandular hairs; internal surface eglandular-strigose; posterior lobe as anterior lobe but ± 18.5 × 3.5 mm including apical spine ± 6.2 mm long; lateral lobes narrower, 13.7–13.9 × 2–2.2 mm, including apical spine 3.7–4.9 mm long. *Corolla* pale bluish-purple, ± 28 mm long (one flower measured), glabrous externally; tube cylindrical, ± 14 mm long, ± 3 mm diameter; limb in weak "4+1" configuration; abaxial lobe offset by ± 3.1 mm, broadly obovate, ± 14.5 × 10.4 mm, apex rounded; lateral lobes obovate, 11–13 × 8.2–8.5 mm, apices obtuse (ratio of abaxial: lateral lobe length ± 1.1–1.3: 1); adaxial lobes elliptic-obovate, 12–13.5 × 6–6.2 mm, apices obtuse. *Stamens* inserted ± 8 mm from base of corolla tube; filaments of long stamens 17–18 mm long, sparsely pubescent at base; anthers ± 2 mm long; short lateral stamens with filaments 1.5–1.7 mm long, with sparse retrorse hairs at base, antherodes ± 0.6 mm long; median staminode ± 0.4 mm long. *Ovary* not seen; style glabrous; stigma linear, 0.45–0.5 mm long. *Capsule* and seeds not seen.

Etymology

Barleria filtuensis is named after the town of Filtu in southern Ethiopia, close to which the three known specimens of this species have been collected.

Distribution

This species is endemic to the Liben Zone, Somali Region of southern Ethiopia (SD floristic region). It has to-date been found along the road from Negele to Filtu. See Fig. 3.

Habitat and Ecology

This species occurs in a mixed open woodland comprising *Senegalia-Vachellia* bushland with *Barbeya oleoides* Schweinf. and some *Terminalia* and *Combretum* spp. on outcrops of limestone, eroding into a whitish grey limestone-rich soil (*Friis et al. 14839*). The ground cover is rich in the local endemic *Wellstedia filtuensis* D.R.Hunt & Lebrun and other relatively rare, endemic species such as *Jatropha horizontalis* M.G.Gilbert. Other associated species include *Senegalia ogadensis* (Chiov.) Kyal. & Boatwr., *Bauhinia ellenbeckii* Harms, *Convolvulus vollesenii* Sebsebe, *Elaeodendron aquifolium* (Fiori) Chiov., *Endostemon tenuiflorus* (Benth.) M.R.Ashby and *Gladiolus lithicola* Goldblatt (I. Friis, pers. comm. 2024). It occurs at 1350–1450 m elevation.

Conservation status

Barleria filtuensis is a highly range-restricted species, currently only known from three localities in close proximity to one another within the Liben Zone of southeast Ethiopia. It has an area of occupancy (AOO) of 4 km^2 whilst the extent of occurrence (EOO) based on a minimum convex hull is below 1 km^2 based on the known collections, and is therefore matched to AOO in accordance with IUCN guidelines. Google Earth imagery indicates intensive agricultural activity to the west of this species' range towards Negele. Dense human settlement can also be observed to the east of this species range which is in close proximity to the small town of Filtu. While the direct impact on *B. filtuensis* is unclear, settlement expansion and agricultural activity may pose a potential threat to this species. Given its extremely small range (treated as a single location) and proximity to anthropogenic pressures, *B. filtuensis* likely qualifies as **Critically Endangered** under criterion B of the IUCN Red List criteria: **CR B1ab(iii)+2ab(iii)**.

Taxonomic notes

Barleria filtuensis is closely allied to another local endemic from close geographic proximity, *B. negeleensis*, but has a very different gestalt and can be readily separated by the distinct morphological characters as outlined in the diagnosis and Table 1. It should be noted that the collection by Ensermu Kelbessa and Aschalew

Table 2. A comparison of the diagnostic characters for separation of *B. filtuensis* and *B. puberulifolia* from *B. negeleensis.*

Character	*B. filtuensis*	*B. negeleensis*	*B. puberulifolia*
Stem indumentum	Young stems sparsely pubescent with long ascending bristly hairs	Young stems pubescent with long ascending bristly hairs or sparsely so	Young stems puberulous
Stem width, basal stems	1.5–3.6 mm	5–8 mm	3–5.2 mm
Longest ray of axillary spines	16–17.5 mm	10–30 mm	27–41 mm
Leaf shape, size and length:width ratio	Linear-lanceolate to -oblanceolate, 55–69 × 5–8 mm (length: width ratio 8.3–11: 1)	Linear-oblong to narrowly oblong-elliptic, 50 – 140 × 10–27 mm (length: width ratio 3.7–5.2: 1)	Lanceolate to obovate or ovate-elliptic, 23–28 × 6.2–11 mm, (leaf length: width ratio 2.5–3.7: 1)
Leaf indumentum	Adaxial surface glabrous; abaxial surface with long somewhat bristly ascending hairs most dense along midrib and margin, hairs 1.4–2.1 mm long	Both surfaces pubescent with bristly ascending hairs at least along margin, sometimes dense on margin, midrib and on main veins beneath, hairs 1.1–2 mm long	Both surfaces puberulent with minute appressed hairs 0.1–0.15 mm long
Veins	3(4) per side, strongly ascending, midrib prominent abaxially and adaxially, lateral veins prominent abaxially	4(5) per side, strongly ascending, midrib and lateral veins prominent abaxially and adaxially	2(3) per side, strongly ascending, inconspicuous
Bract shape and size	Bracts towards base of spike (but excluding basal pairs) lanceolate to linear-lanceolate; 24–24.5 × 3–6 mm including spine tip 1.5–4 mm long; gradually becoming more linear distally, green	Bracts towards base of spike ovate to oblong-elliptic, 22–40 × 8.5–17 mm including prominent grey apical spine 4–8 mm long, becoming oblanceolate distally, pale green tinged purple at the tip	Bracts towards base of spike lanceolate to linear-lanceolate, 21.7–28 × 2.5–6 mm including spine tip 4.2–9 mm long, becoming linear-spinose distally, pale green to brown
Bract indumentum	Long, ascending, bristly eglandular hairs dense on abaxial surface and margin, glabrous adaxially; occasional patent glandular hairs but very infrequent	Densely pubescent with ascending bristly eglandular hairs and long patent glandular hairs adaxially and abaxially	Appressed to patent, white, eglandular hairs both adaxially and abaxially; patent glandular hairs often longer than eglandular hairs but vary in length
Bracteole shape and size	Linear–lanceolate, apex spinose, 19–20 × 1.1–1.5 mm	Variable, those of first flower in dichasium lanceolate to oblanceolate and can resemble the bracts, 15–32 × (2–) 4–7.5 mm, those of lateral flowers in dichasium more linear-lanceolate, (8–) 14–20 × 1– 2.5 mm, apex spinose	Linear, apex spinose, 20–23 × 1.7–2 mm
Bracteole indumentum	Ascending bristly eglandular hairs 1–1.7 mm long and patent, non-glossy glandular hairs 0.4–0.6 mm long	Densely pubescent with ascending bristly eglandular 0.3–0.5 mm and patent, glossy glandular hairs 0.4–1.2 mm long	Patent to retrorse eglandular hairs 0.1–0.2 mm long and patent glandular hairs 0.3–0.8 mm long
Calyx – anterior lobe size and venation	Lanceolate, no visible midrib or lateral veins, ± 16.8 × 3.5 mm including spine tip 6 mm long	Lanceolate, prominent midrib and lateral veins, (11–) 14–17 × 4–6 mm including spine tip 2.5 mm	Lanceolate, prominent midrib and parallel veins, 13.2 × 4 mm including spine tip 3.2 mm
Calyx – anterior lobe indumentum	External surface densely pubescent with ascending eglandular hairs covering surface and shorter glandular hairs concentrated along midrib and distally	External surface densely pubescent with long bristly ascending or appressed eglandular hairs and long patent glossy glandular hairs	External surface with short eglandular hairs and long patent glandular hairs
Corolla indumentum	Glabrous externally	Glabrous externally	Shortly puberulous externally

Getahun (*3997*) appears to be a mixed collection – the lefthand plant on that specimen is true *B. filtuensis* whilst the righthand pieces tend towards *B. quadrispina* in having a less dense indumentum and narrower bracts; these latter plants may be of hybrid origin.

The newly described *Barleria filtuensis* and *B. sebsebei*, together with the recently described *B. negeleensis* (see spp. 3 and 6 below) all occur in close proximity within a phytogeographical transition zone between the Ethiopian highlands and the lowlands of Eastern Ethiopia and Somalia. Another recently described species in the Quadrispina clade, *Barleria ferox* (sp. 7 below) also occurs in a similar transition zone, although it is found considerably further to the northeast than the first three taxa (Figure 3). This transition zone was first documented by Lovett and Friis (1996), who noted a number of characteristic, range-restricted species such as *Barbeya oleoides* (Barbeyaceae), *Cadia purpurea* (G.Piccioli) Aiton (Fabaceae) and *Pistacia aethiopica* Kokwaro (Anacardiaceae). This transition zone was later described by Friis et al. (2010) as a subtype of the vegetation unit "5. Dry evergreen Afromontane forest and grassland complex (DAF)", namely "5d. Transition between Afromontane vegetation and *Acacia-Commiphora* bushland on the Eastern escarpment (DAF/TR)". Friis et al. (2010) noted that this vegetation type is rich in endemic species. The Habitat & Ecology section above notes some of these endemic species associated with *B. filtuensis*. Later, Friis et al. (2022) revised the potential vegetation map of Ethiopia and elevated this transition zone to a stand-alone vegetation unit, namely "Transitional Semi-Evergreen Bushland (TSEB)" (see Figure 4.1 of Friis et al. 2022). The recognition of four species of *Barleria* from the Quadrispina clade within this vegetation unit adds further evidence to its importance for plant endemism.

Additional specimens examined (paratypes)

ETHIOPIA. Sidamo, 107 km from Negelle [Negele] towards Filtu, 05°10'N, 40°32'E, 14 Dec. 1990 (fl.), *Sebsebe D. & Ensermu K. 2690* (ETH!); Sidamo, Borana Awraja, about 110 km from Negelle [Negele] on the road to Filtu, 05°08'30", 40°29'50"E, 20 Dec. 1998 (fl.), *Ensermu K. & Aschalew G. 3997* in part (ETH!) - see note.

3. *Barleria negeleensis* Ensermu & I.Darbysh., Kew Bull. 73(1)-1: 16. 2018.

Type: Ethiopia, Sidamo Region, Borana, 31 km from Negele towards Filtu, 05°13'N, 39°47'E, 14 Dec. 1990, *Sebsebe D. & Ensermu K. 2658* (holotype ETH!; isotype K! [K000963717]).

(=) *Barleria* sp. [= *Sebsebe D. & Ensermu K. 2658*] *sensu* Ensermu in Fl. Ethiopia & Eritrea 6: 416. 2006.

For a full description and illustration, see Ensermu and Darbyshire (2018: 16, Fig. 6).

Distribution

This species is restricted to the southeastern portion of Oromia regional state (BA and SD floristic regions) of southern Ethiopia, centered on the town of Negele. Fig. 3.

Habitat and Ecology

This species occurs in open grassland and grassy-scrub with scattered *Senegalia, Vachellia*, *Combretum*, *Commiphora* and/or *Terminalia* or in denser *Senegalia-Vachellia-Commiphora* woodland with *Barbeya oleoides* Schweinf., in sandy soil overlying granite or on limestone; 1400–1700 m elevation.

Conservation status

This rare and localized species with an EOO of only 2,117 km^2 is assessed as **Endangered** under criteria B: **EN B1ab(iii)+2ab(iii)** on the IUCN Red List (Darbyshire and Roberts 2023). Threats include habitat loss and degradation from both the expansion of human residential infrastructure and the expansion of agriculture.

Taxonomic notes

The collection from Bale Region, *Friis et al. 11071*, is currently considered to be a depauperate specimen of this species, although the inflorescence is less densely hairy than in other flowering specimens, with shorter bristly eglandular hairs, and the leaves dry a darker green tinged purple, whilst the Sidamo material has yellow-green leaves. Further material from the Bale site is desirable; it may be a distinct regional form or a further species in this complex.

For phytogeographic affinities of this species, see note under *Barleria filtuensis*.

Additional specimens examined

ETHIOPIA. Sidamo Region: near Wadera, 6 Jan. 1959 (fr.), *H. F. Mooney 7706* (EA!, ETH!, PRE!); Borana Awraja, 42 km SW of Negele Borana, along the road leading to Wellensu [Wolensu] Ranch, 24 Dec. 1981 (fl.), *Mesfin T. & Tewolde B. G. E. 2636* (ETH!); Bale Region: c. 52 km N of Sidambale Bridge towards Dolo Menna, 5°55'N, 39°37'E, 20 Dec. 2002 (fl.), *I. Friis et al. 11071* (C!, ETH!, K! [K000963716]).

4. *Barleria puberulifolia* Defty & I.Darbysh., **sp. nov.**

Type: Somalia, N Somalia site A/10, 09°56'N, 45°40'E, 23 June 1981 (fl.), *J. B. Gillett & R. M. Watson 23592* (holotype K! [K001295248]; isotype EA! [EA000043816]); Figure 5.

Diagnosis

Barleria puberulifolia is most likely to be confused with *B. negeleensis* but differs in (1) the young stems being puberulous with minute appressed hairs (versus being pubescent with long ascending bristly hairs); (2) the leaves being puberulent with minute appressed hairs 0.1–0.15 mm long (versus pubescent with long ascending bristly hairs 1.1–2 mm long); (3) the leaves having inconspicuous venation with 2 (–3) lateral veins per side (versus having prominent venation with 4 (–5) lateral veins per side); (4) the bracts towards the base of the spike being lanceolate to linear-lanceolate, 21.7–28 × 2.5–6 mm, eventually turning linear-spinose at the apex of the inflorescence (versus the bracts at the base of the spike being ovate to oblong-elliptic, 22–40 × 8.5–17 mm, eventually turning oblanceolate towards the apex of the inflorescence); (5) the corolla being shortly puberulous externally (versus glabrous externally); and (6) the leaves being lanceolate to obovate or ovate-elliptic, 23–28 × 6.2–11 mm, length: width ratio 2.5–3.7: 1 (versus leaves linear-oblong to narrowly oblong-elliptic, 50–140 × 10–27 mm, length: width ratio 3.7–5.2: 1). See Table 2.

Barleria puberulifolia may also be confused with *B. quadrispina*, but it can easily be separated by (1) the leaves being densely puberulous with minute appressed hairs (versus strigose at least on the margin, often also on the veins beneath); (2) the inflorescence being more densely glandular-hairy (versus glandular hairs absent to sparse in the inflorescence except in subsp. *kenyana* where they are more numerous, but not so dense as in *B. puberulifolia*), and (3) the corolla being shortly puberulous externally (versus glabrous externally).

Description

Harshly spiny compact subshrub, 10–30 cm tall; young stems 4-angular, silvery appressed-puberulous, hairs 0.1–0.2 mm long; mature stems woody, up to 3–5.2 mm in diameter. *Axillary spines* numerous, beige-white, stalk 2–14 mm long, 4-rayed, rays of similar length, straight, longest ray 27–41 mm long. *Leaves* on short, ill-defined petioles 1.6–1.7 mm long, these silvery appressed-puberulous; blade lanceolate to obovate, 23–28 × 6.2–11 mm, (length: width ratio 2.5–3.7: 1), base attenuate to obtuse, margin entire, apex acute to slightly attenuate with apical spine 1.1–2.7 mm long, both surfaces densely (sub-) appressed-puberulous, hairs 0.1–0.15 mm long; lateral veins 2 (–3) per side, ascending, inconspicuous. *Inflorescences* terminal, shortly spiciform or subcapitate, 3.5–4.5 cm long, each axil multi-flowered, flowers sessile; bracts towards base of inflorescence lanceolate to linear-lanceolate, 21.5–28 × 2.5–6 mm including spine tip 4–9 mm long, bracts becoming linear-spinose distally, with short appressed to patent white eglandular hairs both adaxially and abaxially and with patent glandular hairs often longer than eglandular hairs but variable in length, 0.2–1 mm long; bracteoles greenish white, linear, spinose, 20–22 × 1.5–2 mm, including spine tip 5–5.5 mm long, with patent to retrorse eglandular hairs 0.1–0.2 mm long and patent glandular hairs 0.3–0.8 mm long. *Calyx* (one calyx measured) pale green–white; anterior lobe lanceolate, ± 13.2 × 4 mm including purple, bifid spine tip 3.2 mm long, external surface with patent long glandular and short eglandular hairs abaxially, midrib and parallel veins prominent internally, only midrib prominent externally; posterior lobe as anterior lobe but ± 15.5 × 5 mm including spine tip 4.1 mm long; lateral lobes narrower, lanceolate to linear-lanceolate, 11.6–11.9 × 1.5–1.6 with spine tip 3.6–3.8 mm long, apices attenuate. *Corolla* white to deep blue, ± 30 mm long (one corolla measured), with short appressed hairs externally, most dense on the throat; tube cylindrical, ± 20 mm long, ± 4.5 mm diameter; limb in "4+1" configuration; abaxial lobe not sufficiently preserved for measurement in specimens examined; lateral lobes obovate, ± 12 × 7 mm, apices acute; adaxial lobes obovate, 12–13.5 × 5.6–5.7 mm, apices broadly acute. *Stamens* inserted ± 6.5 mm from base of corolla tube; filaments of long stamens ± 14.7 mm long, sparsely pubescent at base; anthers 2.5–2.6 mm long; short lateral stamens with filaments 2.2–3.2 mm long, antherodes ± 1 mm long. *Ovary* not seen; style glabrous, ± 21.5 mm long; stigma linear, 0.8–0.9 mm long. *Capsule* (one capsule measured) ± 11.5 mm long including short beak ± 4 mm, external surface with short white hairs distally, glabrous proximally, 2-seeded; seeds ± 5.6 × 4.9 mm, with dense indumentum of wavy golden hygroscopic hairs.

Etymology

The species epithet "*puberulifolia*" refers to the indumentum of minute (sub) appressed hairs on the foliage of this species, an unusual feature in the Quadrispina clade.

Distribution

Barleria puberulifolia is distributed in the Bari, Mudug, Nugal, Sanaag, and Togdheer regions of Somalia (N1, N2, N3 and C1 floristic regions). Fig. 3.

Habitat and Ecology

This species occurs in *Senegalia-Commiphora* bushland and on open rocky areas, including on limestone ridges and slopes, often in cracks in the rock and along drainage lines and small water courses. Associated plants include: *Buxus hildebrandtii* Baill., *Commiphora* spp., *Dodonaea viscosa* Jacq., *Dracaena ombet* Kotschy & Peyr. subsp. *schizantha* (Baker) Bos, *Euryops* sp., *Periploca* sp., *Sideroxylon mascat-*

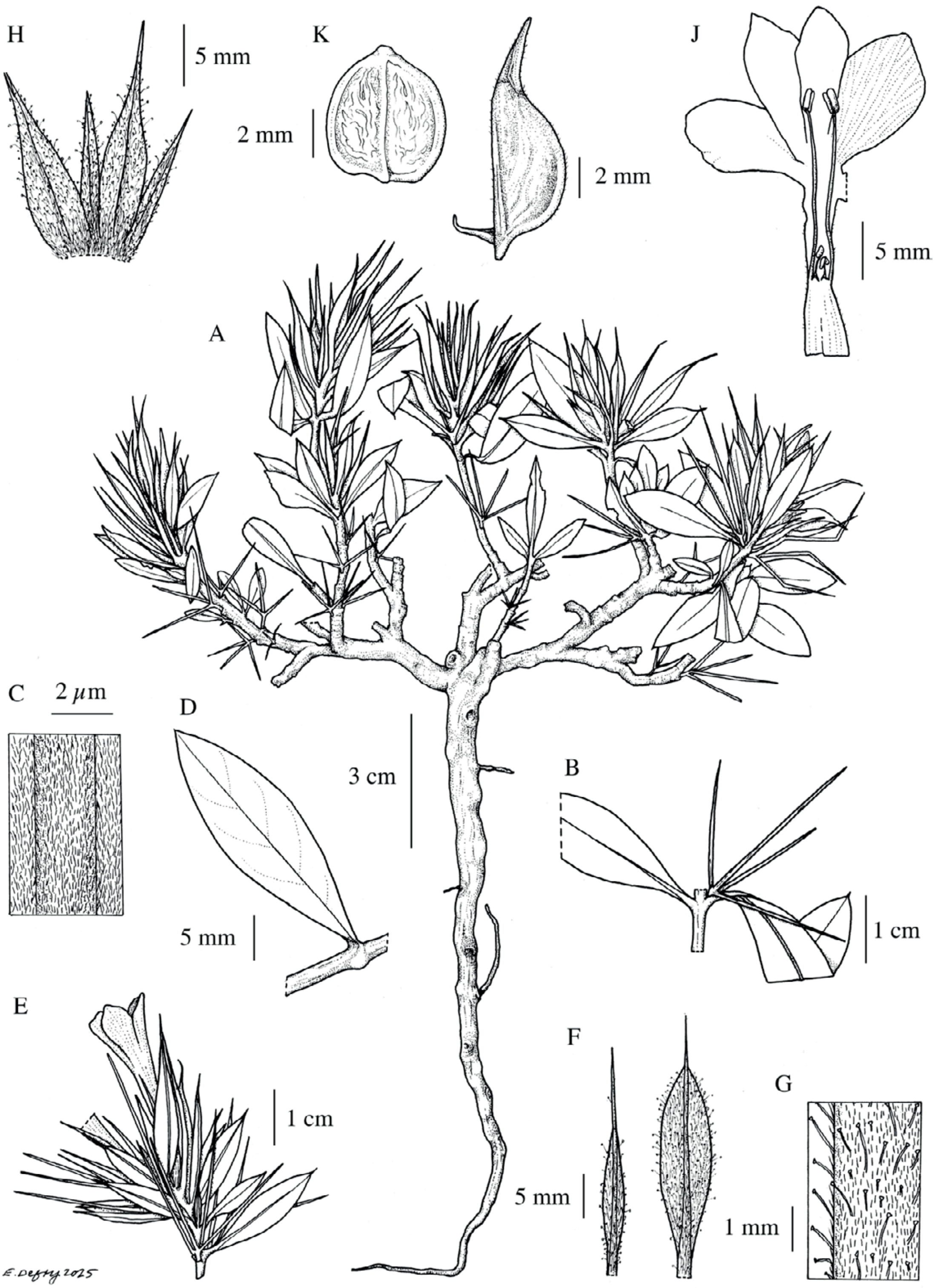

Figure 5. *Barleria puberulifolia*. **A.** Habit, mature stamens and leafy branches, including broken spines. **B.** Stem node with leaves, abaxial surfaces, and axillary spine. **C.** Leaf indumentum, adaxial surface. **D.** Leaf in situ, adaxial surface, indumentum omitted. **E.** Inflorescence, flowering, with axillary spine at base. **F.** Bracteole (l) and bract (r), with indumentum. **G.** Detail of bract indumentum. **H.** Dissected calyx, with indumentum. **J.** Dissected corolla with androecium, abaxial corolla lobe not preserved. **K.** Seed, with hygroscopic hairs, and capsule valve. A–D, F–H. from *J. B. Gillett & R. M. Watson 23592* (K, holotype); E and J. from *C. F. Hemming & R. M. Watson 3309* (K); K. from *P. R. O. Bally & R. Melville 15466* (K). Drawn by Ellie Defty.

ense (A.DC.) T.D.Penn. and *Tarchonanthus camphoratus* L., as well as succulents including *Aloe* spp., *Euphorbia* spp., *Kalanchoe* spp. and *Pyrenacantha malvifolia* Engl. It occurs at elevations of (200–) 750–1590 m.

Conservation status

This species is widespread but highly scattered in northern Somalia, with an extent of occurrence (EOO) of 80,740 km^2 but an area of occupancy (AOO) of only 20 km^2 based on known occurrence data. Despite the relatively large EOO, this species' highly restricted AOO suggests it could be vulnerable to potential threats, although it may also reflect limited botanical exploration in this part of Somalia. The region is affected by low to medium density agropastoralism which can lead to habitat degradation through overgrazing. However, this species' preference for rocky ridges and slopes may afford it some protection from human disturbance. Given its restricted AOO, its estimated 5–6 threat-based locations and the potential threats from agropastoralism, *B. puberulifolia* is likely to qualify as **Vulnerable** under criterion B: **VU B2ab(iii)**.

Taxonomic notes

Hedrén (2006a) noted that this taxon differs from typical *B. quadrispina* in being a low shrub with very short internodes, having greyish-green leaves covered by a dense indumentum of minute appressed hairs and in the bracteoles having a fairly well-developed blade and ± abruptly narrowed into the apical spine and in having patent glandular hairs 0.2–0.3 mm long. He cited the specimens *Lavranos & Carter 24630* (N3), *Hemming & Watson 3309* (N2) and *Gillett et al. 22097* (C1), but we believe this last specimen is cited in error and should have read *Gillett & Watson 23592* (N1). Hedrén (l.c.) maintained these specimens within *B. quadrispina* as he argued that they differ amongst themselves in other characters such as spine length and that they are connected with some forms of *B. quadripsina* and show intermediacy in at least some of these characters. However, we do not find this to be the case and the combination of minute appressed hairs, inconspicuous leaf venation of 2 (–3) veins per side, long glandular hairs and short eglandular hairs on the bracts, bracteoles and calyx and shortly puberulous indumentum on the external surface of the corolla is diagnostic. This new species is also superficially similar to *B. negeleensis* from SE Ethiopia (see above) but the two are readily separated by the characters listed in the diagnosis above.

P. R. O. Bally 9571 (EA! [EA000043817], K! [K001295251]) from 44 miles N of Dusa Mareb in the C1 region of Somalia is similar to this species but it differs in having a spreading puberulous leaf indumentum when mature, larger leaves with more prominent venation beneath and a prominent purple leaf spine tip. Further, more complete material from this population is required to determine if it belongs here or is a distinct species.

Additional specimens examined

SOMALIA. 95 km E of Sinugif, 40 km NW of Eil airstrip, 1 Jan. 1973 (fl.), *P. R. O. Bally 15466* (K! [K001295253]); L76 140 km WSW of Erigavo, 10°24'N, 46°06'E, 27 Nov. 1980 (fl.), *C. F. Hemming & R. M. Watson 3309* (EA! [EA000043815], K! [K001295249]); 114 km N of Garoe on road to Gardo, 5 km S of Dan Goreyo, 08°41'N, 49°18'E, 12 Nov. 1986 (fl.), *J. Lavranos & S. Carter 24630* (K! [K001295250]); Mudug, Garoe–Belet Huen, bei Galcayo, 200 – 300 m, 15 Dec. 1987 (fl.), *B. Gabriel* s.n. (B* [B101161468]); Nogal/Mudug, Gardo – Garoe, 24 March 1989 (fl.), *B. Gabriel s.n.* (B* [B101161476]).

5. *Barleria quadrispina* Lindau in Annuario Reale Ist. Bot. Roma 6: 72. 1896.

Clarke in Fl. Trop. Afr. 5: 147. 1899, pro parte, excl. *Donaldson-Smith s.n.* ex Turfa. Milne-Redhead in Hook. Ic. Pl. 33: t. 3293. 1935. Ensermu in Fl. Ethiopia & Eritrea 6: 416, fig. 166.30. 2006, pro parte. Hedrén in Fl. Somalia 3: 438, fig. 292. 2006, pro parte. Darbyshire in Fl. Trop. East Afr., Acanthaceae (Part 2): 432. 2010.

Type: Ethiopia, Harar, 1889 (st.), *L. Robbecchi-Bricchetti 10* (lectotype B*, chosen by I. Darbyshire in Fl. Trop. East Afr., Acanthaceae (Part 2): 432 [2010], photo. at K!; isolectotype FT! [FT003197]).

Additional syntype, not selected as lectotype: Ethiopia, Vallata di Mil Mil, 9 Jan. 1893 (st.), *D. Riva 1065* (FT! [FT003198]).

(=) *Barleria setigera* Rendle in J. Bot. 34: 395. 1896.

Type: Ethiopia, Darar, 15 Sept. 1894 (fl.), *A. Donaldson-Smith s.n.* (holotype BM! [BM000931070]).

(=) *Barleria setigera* Rendle var. *pumila* Rendle in J. Bot. 34: 396. 1896.

Type: Ethiopia, Okoto, 8 Sept. 1894 (fl.), *A. Donaldson-Smith s.n.* (holotype BM! [BM000931069]).

Description

Compact spiny subshrub 8–40 cm tall; young stems green to brown, 4-angular, largely glabrous or with many short spreading white hairs, nodes often strigose. *Axillary spines* beige-white, subsessile or stalk to 12 mm long, rays 4 (–6), straight or ascending, longest ray 10–29 mm long. *Leaves* sessile or on petioles to 9 mm long; blade oblanceolate, obovate or narrowly oblong-elliptic, (17–) 20–76 × 8–24 mm (length: width ratio 2–6.5: 1), base cuneate or attenuate, apex acute to rounded, mucronate, strigose at least on the margin, often also on the veins beneath, hairs unbranched; lateral veins 3–6 per side. *Inflorescences* terminal, ± densely spiciform or subcapitate, 2–6.5 (–10) cm long, each axil 3–7 flowered when mature, subsessile or peduncle to 2 (–4.5) mm long; bracts of lower axils foliaceous, becoming smaller upwards where green to whitish, (linear-) oblanceolate, 12–40 × 1.5–7 mm (length: width ratio 3.7–9 (–12.5): 1), apex spinose, margin and midrib with coarse appressed to spreading hairs with or without a bulbous base, external surface sometimes with patent glandular hairs, hairs unbranched, broad sessile glands occasional or absent towards base; bracteoles erect or ascending, linear (-lanceolate) or oblanceolate, 9–32 × 0.5–4 mm, short peduncle of lateral cyme branches fused to subtending bracteoles; flowers subsessile or pedicels 3 mm long. *Calyx* greenish-brown or green to glaucous, anterior lobe 5.5–14.5 mm long, basally ovate or lanceolate where 1.5–3 (–4) mm wide, then abruptly or rarely gradually narrowed into a flexible spine, this sometimes bifid, external surface glabrous to eglandular- and/or glandular-pubescent, with or without coarse, ± bulbous-based hairs along margin, venation inconspicuous; posterior lobe as anterior, but 6.5–17 × 1–3.6 mm; lateral lobes 5–12.5 × 0.8–1.2 mm. *Corolla* white, blue or purple, 17–34 mm long, glabrous externally, tube cylindrical, 11.5–20 mm long; limbs in weak "4+1" configuration or subregular, abaxial lobe offset by 0.5–4 mm, oblanceolate, 10–17 × 4.5–12 mm, apex acute; lateral lobes as abaxial lobe but 4–10.5 mm wide; adaxial lobes narrower, 3–8 mm wide, apices obtuse. *Stamens* inserted 4.5–10 mm from base of corolla tube; filaments of long stamens 16–23 mm long, shortly pubescent at least in proximal half; anthers 1.5–2.5 (–3) mm long; short lateral stamens with filaments 1–2.7 mm long, pubescent, antherodes 0.5–0.9 mm long. *Ovary* and style glabrous; stigma 0.4–0.7 mm long. *Capsule* 9–11 mm long, including beak 3–3.5 mm long, glabrous; seeds 3.7–5 × 2.5–4 mm.

Distribution (for species)

This species is widespread within the African portion of the Horn of Africa biodiversity hotspot, where it is known from eastern and northern Ethiopia (AF, BA, GG, HA, SD, SU and TU floristic regions), Somalia (N1, N2, C1, C2, S1 and S2 floristic regions) and northeast Kenya (K1 floristic region). Fig. 6.

Taxonomic and nomenclatural notes (for species)

As noted by Darbyshire et al. (2010), there is some uncertainty over the priority of the names *Barleria quadrispina* and *B. setigera*, both of which were published in 1896. The month of publication of *B. setigera* is noted to be September (in Journal of Botany 34: 393, immediately before the paper of Rendle [1896] where *B. setigera* is described). The month of publication of *B. quadrispina* by Lindau (1896) is not recorded, although the manuscript is marked "finito di stampere il 30 Dicembre 1895" (p. 83; "finished printing on 30 December 1895") and a handwritten note on the Kew copy of this work states "presumably published early 1896". It is therefore reasonable to consider that the name *B. quadrispina* has priority.

a. Barleria quadrispina Lindau, Annuario Reale Ist. Bot. Roma 6 : 72. 1896.

subsp. ***quadrispina***

Description

Leaves obovate to oblanceolate or oblong-elliptic, (17–) 20–56 (–76) mm; length: width ratio 2.3–6.2: 1. *Bracts and bracteoles* typically drying green (-brown) or somewhat glaucous, with coarse eglandular hairs, sometimes bulbous-based along margin, midrib and veins and/or short glandular hairs; short eglandular hairs absent; bract length: width ratio 3.7–9: 1 at midpoint. *Calyx* green or somewhat glaucous; eglandular hairs present along margins, sometimes bulbous based, sometimes with glandular hairs on external surface, or glabrous; anterior lobe 5.5–9.9 × 1.5–1.9 mm, posterior lobe 6.5–10.3 × 1.8–2.5 mm. *Corolla* bluish-purple or white, 17–30 mm long.

Distribution

This subspecies is widespread in Ethiopia, mainly to the east of or within the Rift Valley, (AF, BA, GG, HA, SD and SU floristic regions), but also with one record from west of the Rift in Tigray regional state (TU floristic region). There are also some records from the Togdheer and Woqooyi Galbeed Regions of northern Somalia (N1 floristic region). Fig. 6.

Habitat and Ecology

This subspecies occurs primarily in *Senegalia-Vachellia-Commiphora* bushland and dense or open

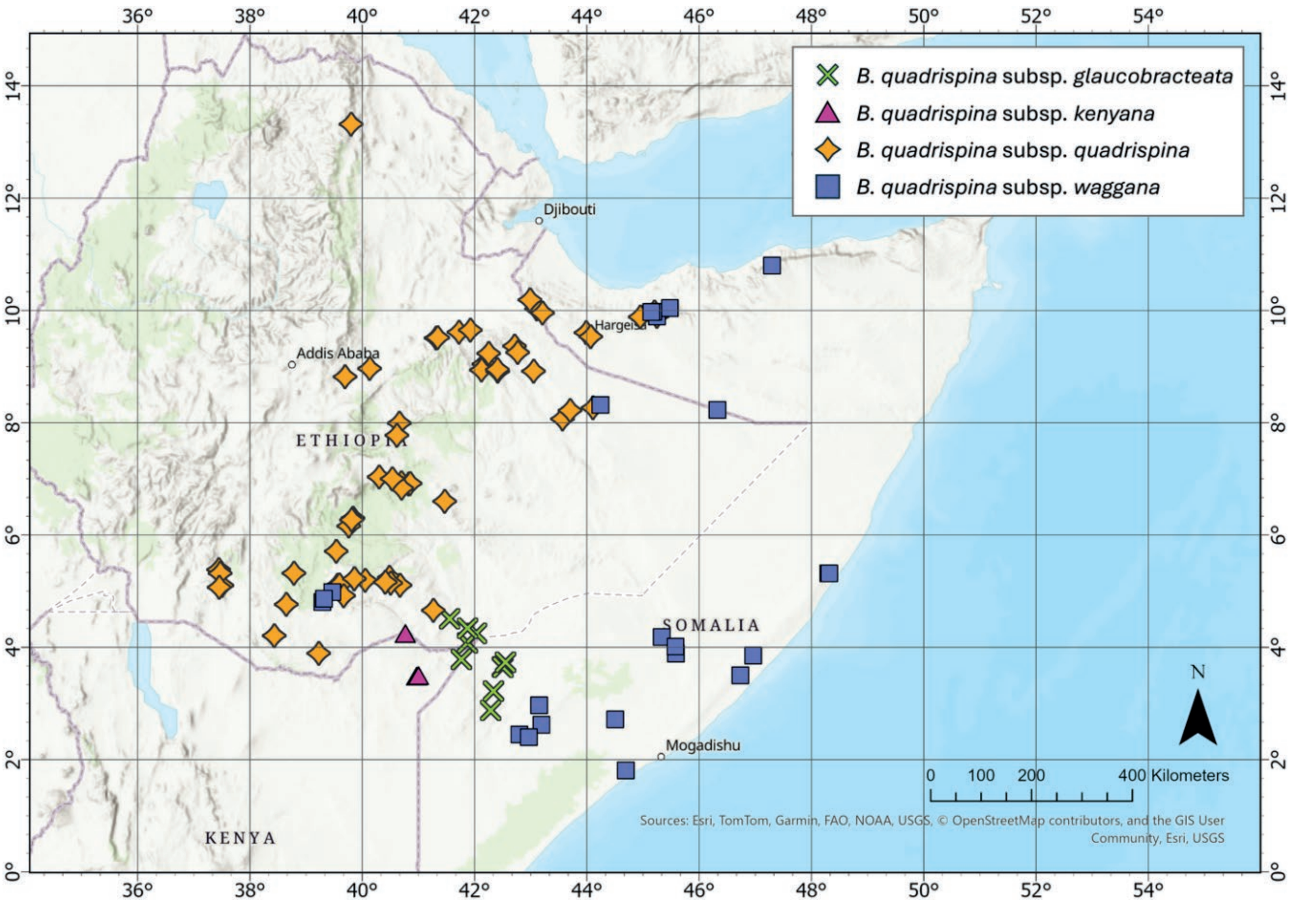

Figure 6. Geographic distribution of the subspecies of *Barleria quadrispina* in northeastern Africa.

thicket, on sandy, gravelly or stony soils including over limestone, at elevations of 250–1780 m.

Conservation notes

This subspecies has an area of occupancy (AOO) of 224 km^2 and an extent of occurrence (EOO) of 493,576 km^2. It is locally common in a range of dry bushland habitats and is assessed as **Least Concern** (**LC**).

Taxonomic notes

The specimen *Friis et al. 10719* is the only collection seen from Tigray floristic region and is disjunct from other populations of *Barleria quadrispina*, being the only population known from west of the Rift Valley. This is from an unusual site near Ab'ala with "limestone pavement", i.e., a flat area with limestone broken up into tile-like sections. This habitat has not been recorded elsewhere in Tigray; the locality is on the eastern escarpment of the Ethiopian highlands, and geological structures that are elsewhere covered by the basalt may be exposed here (I. Friis, pers. comm., 2024). Therefore, it seems correct that this is an isolated record rather than *B. quadrispina* being under-recorded in Tigray.

It should also be noted that the specimens *Puff et al. 820913* (Shewa floristic region), *Friis et al. 12358* (Afar) and *Burger 887* (Harar) are also geographically somewhat disjunct, being located in or on the edge of the Ethiopian Rift Valley. These specimens appear slightly different in gestalt, and tend towards *B. waggana* in having rather numerous bulbous-based hairs on the inflorescence but are otherwise closer to subsp. *quadrispina*.

Additional specimens examined

ETHIOPIA. Jijiga road, without date (fl.), *Imp[erial] Coll[ege] Agric[ulture] D-11* (EA!); Harar Province, Erer River area 60 km W of Dire Dawa on highway to Addis Ababa, 09°31'N, 41°25'E, 11 Sept. 1961 (fl.), *W. Burger 887* (HUHE, K! [K001295184]); 10–5 km N of Midaga, S of Harar, 08°47'N, 42°10'E, 14 Oct. 1962 (fl.), *W. Burger 2200* (K! [K001295180]); S of Midaga, on plateau S of

Harar, 08°47'N, 42°10'E, 14 Oct. 1962 (fl.), *W. Burger 2224* (ETH!, K! [K00129578]); Erer valley 22 km SE of Harar on highway to Djidjiga, 09°14'N, 42°15'E, 18 Oct. 1962 (fl.), *W. Burger 2224* (K! [K00129579]); Haraghie [Harar] Province, 6 km NW of Aware, 69 km SE of Degehabur, 11 June 1973 (fl.), *M. G. Gilbert 2061* (EA!, ETH!, K! [K001295177]); Harerge [Harar], 68 km from Dire Dawa on road through Afdem to Addis Ababa, 1 km from Gota, 24 Sept. 1980, *Ensermu K. & Tamirat B. 360a* (UPS!); Sidamo, 33 km from Neghelle [Negele], along the road to Filtu, 20 May 1982 (fl.), *I. Friis, Mesfin T. & K. Vollesen 3156* (ETH!); at the Wells El Siro, 11 km from the turn off from the Neghelle [Negele]–Filtu road, 85 km from Neghelle [Negele], 22 May 1982 (fl.), *I. Friis, Mesfin T. & K. Vollesen 3193* (ETH!, K! [K001295194]); Yerer & Kereyu Awr., 162 km from Addis Ababa, towards Awash Stn., Caldera (nr. "Garibaldi pass"), 08°51'N, 39°58'E, 13 Sept. 1982 (fl.), *C. Puff, Ensermu K. & J. Dawe 820913-2/11* (ETH!, K! [K001295188]); Bale, Web valley at Sof Omar, 6°50'N, 40°42'E, 9 Nov. 1982, *M. Hedrén 668* (UPS!); Bale, Goro, 7°00'N, 40°32'E, 9 Nov. 1982, *M. Hedrén 670* (UPS!); 65 km from Negele on road to Filtu, 05°11'N, 40°08'E, 16 May 1983 (fl.), *M. G. Gilbert, Ensermu K. & K. Vollesen 7439* (ETH!, K! [K001295198]); Sidamo, El Siro Water-holes, 101 km from Negele, 11 km N of road to Filtu, 04°53'N, 40°54'E, 22 May 1983 (fl.), *M. G. Gilbert, Ensermu K. & K. Vollesen 7720* (ETH!, K! [K001295196], UPS!); El Siro Water-holes, 101 km from Negele, 11 km N of road to Filtu, 04°53'N, 40°54'E, 22 May 1983 (fl.), *M. G. Gilbert, Ensermu K. & K. Vollesen 7722* (ETH!, K! [K001295197], UPS!); Bale, 97 km from Robi on road to Ghinir, 06°55'N, 40°47'E, 27 May 1983 (fl.), *M. G. Gilbert, Ensermu K. & K. Vollesen 7832* (ETH!, K! [K001295192]); Bale, 2 km before Sof Omar in Web Gorge, 36 km from Ghinir on road to Robi, 06°54'N, 40°50'E, 28 May 1983 (fl.), *M. G. Gilbert, Ensermu K. & K. Vollesen 7856* (ETH!, K! [K001295189], UPS!); Bale, 14 km E of Goro on road from Ginir & Sof Omar (in Web Gorge) to Robe, 06°55'N, 40°42'E, 1 June 1983 (fl.), *M. G. Gilbert, Ensermu K. & K. Vollesen 8017* (ETH!, K! [K001295190]); Harerge [Harar] Region, Dire Dawa, Isa and Gurgura Awr., 4 km from Dire Dawa on the road to Harer/Addis Abeba, 18 Sept. 1985 (fl.), *Ensermu K. 1350* (ETH!); Bale Region, Delo Awraja, ca. 19 km on Dello Mena – Negelle [Negele] Borena road, 06°29'N, 39°44'E, 9 June 1986 (fl.), *Mesfin T. 4486* (ETH); Harar, Gursum Awr., 35 km S of Babile on the road to Fik, 21 Jan. 1987 (fl.), *Ensermu K. & Petros E. 1899A* (ETH!); *idem*, *Ensermu K. & Petros E. 1899B* (ETH!); Wabe Awr., road Robe to Ginnir (via Goro, 58 km and S of Omar), km 104 – 106 (Sof Omar area; Weyb gorge), 06°55'N, 40°51'E, 12 May 1987 (fl.), *C. Puff et al. 870512-4/17* (ETH!); Hararghe [Harar], Harer Zuriya Wr., 58 km from Harer (34 km from Fedis) on the road to Midega, 23 Sept. 1987 (fl.), *Ensermu K. & Petros E. 1960A* (ETH!); *idem*, *Ensermu K. & Petros E. 1960B* (ETH!); Bale, 38 km from Goro towards Sof Omar and Ginir, 07°02'N, 40°18'E, 8 Nov. 1988 (fl.), *I. Friis, A. Michelsen & Sebsebe D. 5760* (ETH!); Awash National Park, close to Gotu, Park headquarters, 29 Sept. 1989 (fl.), *P. Nystrom 72* (ETH!); Gama Gofa, 6 km from Konso on road to Arba Minch, 05°23'N, 37°11'E, 8 Oct. 1989 (fl.), *M. G. Gilbert & S. Phillips 9140* (ETH!, K! [K001295206], UPS!); Sidamo, Welensu cattle Ranch, 68 km S of Negelle [Negele] (42 km off the main Negelle [Negele] – Melka Guba Road after 26 km), 04°55'N, 39°40'E, 19 Dec. 1990 (fl.), *Sebsebe D. & Ensermu K. 2814* (ETH!); Sidamo, 30 km from Mega towards Negelle [Negele], 04°12'N, 38°20'E, 20 Dec. 1990 (bud), *Sebsebe D. & Ensermu K. 2864* (ETH!); Eastern Hararghe [Harar] region, Dhurwale, 24 km SW of Kebri Beyah, 8°55'N, 43°03'E, 3 Nov. 1992 (bud), *P. Kuchar* & *Mahdi M. Kidar 18120* (ETH!); Eastern Hararghe [Harar] Region, Jijiga, 10 km S on highway from Xadow (Hado), 09°18'N, 42°39'E, 5 Nov. 1992 (fr.), *P. Kuchar & Mahdi M. Kidar 18203* (ETH!); *idem*, , *P. Kuchar & M. Kidar 18216* (ETH!); Eastern Haraghe [Harar] Region, Jijiga, Ghiba, 11 km SSW of Jijiga, 09°15'N, 42°46'E, 27 Oct. 1993 (fl.), *P. Kuchar & Mahdi M. Kidar 19894* (ETH!); *idem*, *P. Kuchar & Mahdi M. Kidar 19895* (ETH!); Eastern Hararghe [Harar] Region, 17 km S of Dhegabur, 08°04'N, 43°34'E, 12 Nov. 1993 (fl.), *P. Kuchar & Mahdi M. Kidar 20091* (ETH!); Eastern Hararghe [Harar] Region, 16 km on rd from Dhegabur to Falfal, 08°13'N, 43°42'E, 24 Nov. 1993 (fl.), *P. Kuchar & Mahdi M. Kidar 20313* (ETH!); Bale, 32–33 km from Dalo Manna on the road to Negelle [Negele], 27 May 1994 (fl.), *Ensermu K. & Melaku W. 2817* (ETH!); Sidamo, Borana, 18 km on the Filtu–Negelle [Negele] road, 12 May 1995 (fl.), *Ensermu K., Z. Gowler & Lemessa K. 3223* (ETH!); Sidamo, Borana, 68–70 km from Negelle [Negele] around the ?deroofed cattle ranch buildings, 14 May 1995 (fl.), *Ensermu K., Z. Gowler & Lemessa K. 3242* (ETH!); Sidamo, 1.2 km SE of Filtu on the road to Bokol Mayo, 24 May 1996 (bud), *Ensermu K. & Dessalegn D. 3656* (ETH!); Sidamo Region, ca. 65 km E of Yavello on the road to Arero, 04°46'N, 38°37'E, 11 Dec. 1997 (fl.), *I. Friis et al. 8550* (ETH!, K! [K001295201]); Sidamo Region, ca. 50 km N of Moyale along the tract to Wachile and past El Gof, 03°57'N, 39°05'E, 21 Dec. 1997 (bud), *I. Friis et al. 8770* (ETH!, K! [K001295208]); Sidamo Region, ca. 10 km from Brindi along the new road to Teltele, 05°06'N, 37°30'E, 9 Dec. 1998 (fl.), *I. Friis et al. 9367* (ETH!, K! [K001295207]); Sidamo, 33–35 km from

Negelle [Negele] on the road to Filtu, 1 June 2001 (fl.), *Ensermu K.& Assefa H. 4361* (ETH!); ca. 10 km E of Ab'ala on a track leading into the Afar and said ultimately to lead to Afrera (Afdera), 13°19'N, 39°48'E, 17 Oct. 2001 (fl.), *I. Friis et al. 10719* (K! [K001295183], UPS!); Bale region, ca. 10 km S of Dolo Menna (Masslo) towards Sidambale Bridge, 06°18'N, 39°50'E, 21 Dec. 2002 (fl.), *I. Friis et al. 11077* (K! [K001295191]); ca. 15 km towards Wolensu from turn off from the road from Negelle [Negele] towards Melka Guba, 05°01'N, 39°46'E, 23 Dec. 2002 (fl.), *I. Friis et al. 11105* (K! [K001295200]); ca. 15 km towards Wolensu from turn off from the road from Negelle [Negele] towards Melka Guba, 05°01'N, 39°46'E, 23 Dec. 2002 (fl.), *I. Friis et al. 11106* (K! [K0012952199]); Oromiya Region, Sidamo, 28 km on Melka Guba road from turn off from Filtu road, 05°06'N, 39°34'E, 2 Oct. 2003 (fl.), *S. Bidgood et al. 4962* (K! [K001295205]); 5 km W of Awash, 08°57.50'N, 40°07.50'E, 5 Oct. 2006 (fl.), *I. Friis, Wege A. & Ermias G. 12358* (K! [K001295181], UPS!); 10 km NE of Dire Dawa towards Djibouti, 09°38.90'N, 41°55.40'E, 9 Oct. 2006, *I. Friis, Wege A. & Ermias G. 12392* (K! [K001295182]); Sidamo, 8 km NE of Teltele towards Brindi and Yavello, 05°01'N, 39°46'E, 24 Nov. 2010 (fl.), *I. Friis et al. 13874* (K! [K001295204]); Sidamo, 80 km E of Agere Mariam on road to Shakiso, 05°19.10'N, 38°46.90'E, 21 Nov. 2011 (fl.), *I. Friis et al. 14091* (K! [K001295203]); Gamo Gofa, 3.5 km SE of Konso on road to Yavello, 05°19'N, 37°27.60'E, 23 Nov. 2011 (fl.), *I. Friis et al. 14134* (K! [K001295202]); Sidamo, at Sidambale Bridge, 05°42.50'N, 39°32.10'E, 4 Dec. 2012 (fl.), *I. Friis et al. 14761* (K! [K001295195]); Bale, Sheik Hussein to Methara, at bridge across the Webi Schebele River, 07°46.28'N, 40°36.90'E, 10 Dec. 2013 (fl.), *I. Friis et al. 15093* (K! [K001295828]); Harar, Chisi / Shube Mts, north-eastern foothills, 07°58.90'N, 40°39.30'E, 10 Nov. 2015 (fl), *I. Friis, Wege A. & Ermias G. 15650* (K! [K001295827]); Bale, road Ginir–Imi, 115 km E of Ginir (just W of Lele Hills), 06°35.90'N, 41°28'E, 17 Nov. 2015 (fl.), *I. Friis, Wege A. & Ermias G. 15701* (K! [K001295826]). - **SOMALIA.** Hargeisa, 09°34'N, 44°01'E, 23 Sept. 1932 (fl.), *J. B. Gillett 3994* (K! [K001295219]); Hagare, NW of Borama, 10°12'N, 42°53'E, Aug. 1933 (fl.), *H. C. Godding 82* (K! [K001295221]); Hargeisa, Locust Survey Camp, 20 Oct. 1949 (fl.), *K. M. Guichard in E.A.H. 10682* (EA! [EA000043805], K! [K001295223]); 8 miles NW of Borama, 4 Oct. 1954 (fl.), *P. R. O. Bally 9954* (EA! [EA000043807], K! [K001295226]); Hargeisa, 8 Oct. 1954 (fl.), *P. R. O. Bally 10007* (K! [K001295224]); Wagger Mt., at foot of southern slope, 26 Oct. 1954 (fl.), *P. R. O. Bally 10231* (K! [K001295222]); Garabgui (Karskoi) Hill, S of Upper Sheik, 8 Oct. 1957 (fl.), *P. R. O. Bally 11804* (K! [K001295225]); Hargeisa (Desert Locust Survey Base), Oct. 1961 (fl.), *C. F. Hemming 2270* (EA! [EA000043803], K! [K001295220]); Togdheer, Sheikh, Bokh reserve, near water point, 09°53'N, 44°57'E, 20 Nov. 1979 (fl.), *O. J. Hansen, H. Heemstra & Abukar Sheikh 6467* (EA! [EA000043802], K! [K001295217]); Borama, May 1972 (fl.), *J. R. I. Wood S/72/91* (EA! [EA000043819], K! [K001295218]).

b. Barleria quadrispina Lindau subsp. ***waggana*** (Rendle) Defty & I.Darbysh., **comb. & stat. nov.**

(≡) *Barleria waggana* Rendle in J. Bot. 35: 377. 1897. C. B. Clarke in Fl. Trop. Afr. 5: 148. 1899.

Type: Somalia, Wagar [Wagga] Mt, 1897 (fl.), *E. Lort-Phillips s.n.* (holotype BM! [BM000931068]).

Description

Leaves mainly obovate, occasionally oblanceolate, 21–42 (–60) mm long; length: width ratio 2–2.7 (–3.7): 1. *Bracts and bracteoles* green, with bulbous-based eglandular hairs numerous along the margin, surface with long eglandular hairs only, glandular hairs and short eglandular hairs absent; bract length: width ratio 5.7–9 (–11.7): 1 at midpoint. *Calyx* green; marginal eglandular hairs with bulbous base; anterior lobe 12–14 × 1.8–2 mm, posterior lobe 14–16 × 2–2.4 mm. *Corolla* always bluish-purple, 18–23 (–30) mm long.

Distribution

This subspecies is recorded from Aware in eastern Ethiopia and the Malka Guba area of southern Ethiopia (HA and SD floristic regions respectively) and is widespread in Somalia (N1, N2, C1, C2, S1 and S2 floristic regions). Fig 6.

Habitat and Ecology

This subspecies occurs primarily in *Senegalia-Vachellia-Commiphora* dominated open bushland on coarse sandy soil. It is also recorded from granite and limestone slopes growing in shallow, stony or silty soil, at elevations of 80–850 m.

Conservation notes

This species has an area of occupancy (AOO) of 76 km^2 and an extent of occurrence (EOO) of 551,967 km^2. It is locally common in a range of dry bushland habitats, and is assessed as **Least Concern** (**LC**).

Taxonomic notes

Subsp. *waggana* is usually easily separated from subsp. *quadrispina* in having a more densely and conspicuously hairy inflorescence with long bristly eglandular hairs, those along the margins of the bracts, bracteoles and calyces having a bulbous base; and in having usually short, obovate leaves. The two subspecies are mainly allopatric but they meet in northern Somalia (Somaliland) including at the type locality for subsp. *waggana*, "Wagga Mountain" where P. R. O. Bally has collected both taxa. Further, an isolated population of subsp. *waggana* around Malka Guba in Sidamo floristic region is well within the range of subsp. *quadrispina*, but this population is a close match to other populations of subsp. *waggana*. This subspecies may be more widespread in eastern Ethiopia which is heavily underbotanised at present.

Additional specimens examined

ETHIOPIA. Melca Guba [Malka Guba], at the Dawa Parma River, 16 May 1982 (fl.), *I. Friis, Mesfin T. & K. Vollesen 3002* (ETH!, K! [K001295209]); Eastern Haraghe [Harar] Region, Aware, 12 km from Aware, on road to Rabasso, 08°19'N, 44°14.5'E, 20 June 1993 (fl.), *P. Kuchar & Mahdi M. Kidar 19330* (ETH!); Sidamo, Malka Guba, 93 km from Negelle [Negele] to Wachile and Mega, 30 May 1996 (fl.), *Ensermu K. & Dessalegn D. 3793* (ETH!); Sidamo, 87 km from Negelle [Negele] on the road to Malka Guba, 04°59'N, 39°28'E, 5 June 2001 (fl.), *Ensermu K. & Assefa H. 4481* (ETH!). - **SOMALIA.** Golis range, 1895 (fr), *E. Lort Phillips s.n.* (K! [K001295233]); between Walwal & Sirauw, 27 Nov. 1944 (fl.), *P. E. Glover & H. B. Gilliland 410* (BM!, EA! [EA000043812], K! [K001295229]); Wagga Mt, at foot of S. slope, 26 Oct. 1954 (fl.), *P. R. O. Bally 10231A* (K! [K001295226]); Bohodle [Buuhoodle], S Border Road., 7 Dec. 1959 (fl.), *C. Ashall in E.A. 11927* (EA! [EA000043814], K! [K001295231]); Wogr [Wagga Mountain] near Sheikh, Nov. 1972 (fl.), *J. R. I. Wood S/72/99* (EA! [EA000043806], K! [K001295227]); 4 km N of Bulo Burti [Buloburde], 23 Dec. 1972 (fl.), *P. R. O. Bally & R. Melville 15292* (K! [K001295238]); site 'b', Janaale area, 3 Jan. 1978, *K. J. Virgo 34* (K! [K001295243]); slopes east of Gawan village, 05°19'N, 48°18'E, 30 May 1979 (fl.), *J. B. Gillett, C. F. Hemming & R. M. Watson 22257* (EA! [EA000043823], K! [K001295237]); Bay region, 2°57'N, 43°05'E, 17 Feb. 1982 (fl.), *J. J. Beckett & R. White 1794* (EA! [EA000043818]); crossroads 84 km NE of Haji Ali, 03°30.5'N, 46°44.5'E, 6 June 1983 (fl.), *J. B. Gillett & C. F. Hemming 24575* (EA! [EA000043820], K! [K001295236]); Hiiraan, Bulo Burti to Halgan, June 1984, *P. Kuchar 16233* (EA! [EA000043813], UPS!); Hiiraan Region, Bulo Burte [Buloburde] District, 17 km NNE of Buqda Caqable [Buq Aqable], 04°11'N, 45°20'E, 4 July 1986, *P. Kuchar 17068* (EA! [EA000043808], FT!, K! [K001295234], UPS!); Mudug, E of Gawen, 29–30 km on road between Hobyo and Wisil, 5°19'N, 48°19'E, 28 May 1989, *M. Thulin & Abdi M. Dahir 6669* (UPS!); Galguduud, 18 km on road from Masagaweyn to Bud Bud, 03°50'N, 46°58'E, 10 May 1990 (fl.), *M. Thulin, M. Hedrén & Abdi M. Dahir 7420* (EA! [EA000043811], FT!, K! [K001295235], UPS!); Bay, 49 km from Buurhakaba [Burhakaba] on road to Muqdisho [Mogadishu], 02°43'N, 44°30'E, 16 May 1990 (fl.), *M. Thulin, M. Hedrén & Abdi M. Dahir 7471* (EA! [EA000043809], FT!, K! [K001295241], UPS!); Bay, 80 km on road from Baydhabo [Baidoa] to Diinsoor [Dinsoor], 02°40'N, 43°14'E, 19 May 1990 (fl.), *M. Thulin, M. Hedrén & Abdi M. Dahir 7589* (EA! [EA000043810], FT!, K! [K001295240], UPS!); Bay, Buur Diinsoor, ca. 3 km SW of Diinsoor, 2°24'N, 42°58'E, 20 May 1990, *M. Thulin, M. Hedrén & Abdi M. Dahir 7638* (UPS!); Bay, ca. 20 km NW of Diinsoor [Dinsoor], area around Kurman village, 02°28'N, 42°48'E, 21 May 1990 (fl.), *M. Thulin, M. Hedrén & Abdi M. Dahir 7691* (K! [K001295242], UPS!); Bay, 39 km from Awdiinle to Qansaxdheere, 2°58'N, 43°09'E, 23 May 1990, *M. Thulin. M. Hedrén & Abdi M. Dahir 7759* (UPS!).

c. *Barleria quadrispina* Lindau subsp. ***glaucobracteata*** (Hedrén) Defty & I.Darbysh., **comb. & stat. nov.**

(≡) *Barleria glaucobracteata* Hedrén in Willdenowia 36: 758. 2006. Hedrén in Fl. Somalia 3: 441. 2006.

Type: Somalia, Gedo Region, 7–8 km S of Luuq, 03°44'N, 42°33'E, 26 May 1988 (fl.), *Somali Medicinal Plant Project SMP 210* (holotype UPS!; isotype K! [K000430890]).

Description

Leaves oblanceolate or sometimes narrowly oblong-elliptic, (37–) 45–60 mm long; length: width ratio 3.2–3.8 (–4.6): 1. *Bracts and bracteoles* glaucous to whitish in dry state, with bulbous-based eglandular hairs along the margin, surface with short glandular hairs and with or without short eglandular hairs; length: width ratio 5.3–9 (–12.5): 1. *Calyx* glaucous to white; glabrous or occasionally very few glandular hairs on external surface; anterior lobe 11.8–13 × 1.8–2.2 mm, posterior lobe 13.7–17 × 1.8–2.4 mm. *Corolla* white, 28–34 mm long.

Distribution

This subspecies extends along the Jubba River catchment and is known from the southern Somali regional state of southern Ethiopia (SD floristic region), Gedo Region in Somalia (S1 floristic region), and Mandera District in Kenya (K1 floristic region), all in close proximity to the international borders between the three countries. Fig 6.

Habitat and Ecology

This subspecies is recorded from *Senegalia-Commiphora*, *Commiphora-Boswellia-Euphorbia* and other forms of bushland (e.g., with *Anisotes*, *Combretum*, *Cordia*, *Grewia*, *Jatropha*, *Lannea*, *Sesamothamnus* and *Ziziphus* spp.), typically on stony (-sandy) to gravelly soils over limestone or gypsum, at 150–500 m elevation. It has also been recorded in close proximity to riverine areas.

Conservation status

This subspecies has an area of occupancy (AOO) of 40 km^2 and an extent of occurrence (EOO) of 8,382 km^2. As such, it falls within the range threshold for Vulnerable (VU) under criterion B1 or Endangered (EN) under criteria B2 on the IUCN Red List. Overgrazing and collecting of wood for charcoal, firewood and house building pose a threat to its dry bushland habitats and have led to habitat degradation. This has been periodically enhanced by the migration of refugees and erection of refugee camps in the border areas between Somalia, Ethiopia and Kenya. We estimate 8–9 threat-based locations for this subspecies and, with a continuing decline in extent and quality of habitat, we therefore assess this subspecies as **Vulnerable** under criterion B: **VU B1ab(iii)+2ab(iii)**.

Taxonomic notes

As noted by Darbyshire et al. (2010), this form from the Ethiopia-Kenya-Somalia border region is distinctive in its strikingly pale bracts, bracteoles and calyces. It is also always a low-growing dwarf shrublet with dense foliage of oblanceolate to narrowly oblong-elliptic leaves and has white flowers that are at the larger end of the size range for *B. quadrispina*. This combination of characters is diagnostic as a distinct regional subspecies.

Additional specimens examined

ETHIOPIA. Sidamo, 24 km SW of Dolo on track to Suftu, 04°04'N, 39°32'E, 19 May 1983 (fl.), *M. G. Gilbert, Ensermu K. & K. Vollesen 7590* (ETH!, K! [K001295210]); Sidamo, 1.5 km from Bokol Mayo towards Dolo Odo, 15 Dec. 1990 (fl.), *Sebsebe D. & Ensermu K. 2705* (ETH!); Sidamo, 13 km from Dolo Odo to Dolo Bay (2 km off the main road), 04°13'N, 42°09'E, 16 Dec. 1990 (fl.), *Sebsebe D. & Ensermu K. 2744A* (ETH!); Sidamo, 30.5 km NW of Dolo along the road to Bokol Mayo, 25 May 1996 (fl.), *Ensermu K. & Dessalegn D. 3709* (ETH!); 27.7 km NW of Bokol Mayo along the road to Filtu, 109.3 km before Filtu, 27 May 1996 (fl.), *Ensermu K. & Dessalegn D. 3732* (ETH!). - **KENYA.** 18 km SW of Mandera, 13 Dec. 1971 (fl.), *P. R. O. Bally & A. R. Smith B14586* (EA!, K! [K004590691]). - **SOMALIA.** 54 km S of Garba Harre [Garbahare] on Bardera rd., 02°53'N, 42°17'E, 14/15 June 1983 (fl.), *J. B. Gillett & C. F. Hemming 24772* (EA! [EA000043821], K! [K001295212]); JESS Site 61 east of R. Jubba, 17 km from Luuq bridge on 195°, 03°40'N, 42°30'E, 5 July 1987 (fl.), *C. F. Hemming & I. Deshmukh. JESS 270* (EA! [EA000043800], K! [K001295254]); JESS Site 68, E of R. Jubba, 16.5 km from Luuq bridge on 200°, 03°40'N, 42°30'E, 9 July 1987 (fl.), *C. F. Hemming & I. Deshmukh. JESS 323* (EA! [EA000043801], K! [K001295246]); Gedo, 20 km on road between Garbaharrey [Garbahare] and Qansaxdheere [Qansahdhere], 5 June 1989 (fl.), *M. Thulin & Bashir A. Mohamed 6918* (K! [K001295244], UPS!).

d. Barleria quadrispina Lindau subsp. ***kenyana*** Defty & I.Darbysh., **subsp. nov.**

Type: Kenya, 55 km SSW of Rhamu, 14 Dec. 1971 (fl.), *P. R. O. Bally & A. R. Smith B14596* (holotype K! [K004590692]; isotypes BR! [BR0000019231198], EA!).

Description [Diagnosis]

Leaves lanceolate to narrowly oblong-elliptic, 60–107 mm long; length: width ratio 4–5: 1. *Bracts and bracteoles* green (-brown) to somewhat glaucous in dry state, with long glandular hairs and short eglandular hairs on surface; bract length: width ratio 9.6–10: 1 at midpoint. *Calyx* greenish-brown or turning whitish, with long glandular hairs and fine short eglandular hairs on external surface; anterior lobe 11.2–13 × 2.6–3 mm, occasionally bifid, posterior lobe (11.8–) 15–15.7 × 3–3.6 mm. *Corolla* bluish-purple or white, 26–32 mm long.

Distribution

This subspecies is currently only known from Mandera County in northeastern Kenya (K1 floristic region). Fig. 6.

Habitat and Ecology

This subspecies is recorded from dry *Senegalia-Vachellia-Commiphora* and mixed bushland and on rocky ground, at ca. 600–800 m elevation. It potentially occurs on limestone; *Gilbert & Thulin 1628* is recorded from a site where the foot of the hills supports bushland on limestone with *Ipomoea donaldsonii* Rendle, *Euphorbia cuneata* Vahl and various *Senegalia, Vachellia* and *Commiphora* with scattered trees of *Delonix elata* (L.) Gamble and *Terminalia* sp.; the collection of this *Barleria* was recorded from the "lower slopes" at this site.

Conservation status

Based upon currently know observation data, this subspecies has an area of occupancy (AOO) of 12 km^2 and an extent of occurrence (EOO) of 162 km^2 and is known from only three collecting localities in Mandera District, Kenya, which are treated as separate locations. Satellite imagery shows little habitat degradation within the range of this subspecies, with agricultural activity and urban development observed in close proximity to only one of the locations. However, further botanical exploration is needed for this subspecies as data is limited and botanical exploration has been restricted to date. We therefore currently assess this subspecies as **Data Deficient** (**DD**).

Taxonomic notes

This subspecies is separated from the other subspecies of *Barleria quadrispina* by the combination of its narrow leaves and rather numerous glandular hairs on the inflorescence. It warrants further collection to determine whether *kenyana* truly belongs as a subspecies to *B. quadrispina* or if it is a distinct species. It should be noted that the collection *Kirrika 118* is unusual in being a robust, large-leaved plant with a rather laxly branched inflorescence with pale axes and calyces, not observed in the two other specimens of this subspecies; it is possible that these inflorescences are somewhat malformed.

Additional specimens examined

KENYA. Dawa River, Murri, 30 June 1951 (fl.), *E. P. Kirrika 118* (EA!, K! [K004590694], PRE!); Mandera District, 48 km on the Ramu [Rhamu] – El Wak road, 03°31'N, 41°00'E, 9/10 May 1978 (fl.), *M. G. Gilbert & M. Thulin 1628* (EA!, K! [K004590693], UPS!).

6. *Barleria sebsebei* Defty & I.Darbysh., **sp. nov.**

Type: Ethiopia, Sidamo, Curre Liban, 28 km from junction of roads from Filtu & Wachile to Negele, 05°06'N, 39°32'E, 16 June 1986 (fl.), *M. G. Gilbert, Sebsebe D. & K. Vollesen 8257* (holotype K! [K001295213]; isotypes ETH!, UPS!); Figure 7.

Diagnosis

Barleria sebsebei is most likely to be confused with *B. quadrispina,* more specifically, subsp. *quadrispina* but differs in (1) the leaves being broadly elliptic to orbicular or occasionally ovate, 22–39 mm wide with a length: width ratio of 1.2–1.7: 1 (versus leaves narrower, 4–16 mm wide with length: width ratio 2.3–6.2: 1); (2) always having many and conspicuous broad sessile glands at the base of the bracts and bracteoles (versus sessile glands absent or rarely few present and inconspicuous); and (3) having a corolla length of 30–37 mm (versus 17–30 mm); see Table 1. Also similar to *Barleria ferox* but differing in (1) the axillary spines being less stout, sessile or stalked for up to 2 mm, with the longest rays being 11–22 (–29) mm long (versus axillary spines very stout, stalked for (4–) 8–16 mm, longest rays typically 22–32 mm long); (2) the leaves being broadly elliptic to suborbicular or occasionally ovate, 22–39 mm wide, length: width ratio 1.2–1.7: 1, with a minute apical spine up to 1 mm long (versus leaves oblong-elliptic or -obovate, 13–25 mm wide, length: width ratio 1.9–2.1: 1, apical spine 2–3 mm long); and (3) the anterior and posterior calyx lobes being lanceolate, being more gradually narrowed into the long apical seta, ± 8.5–11 mm long at flowering, external surface glabrous or with short ascending to appressed eglandular hairs concentrated proximally along midrib (versus anterior and posterior calyx lobes broadly ovate and abruptly narrowed into short apical seta, 4.2–5.5 mm long at flowering, external surface with scattered broad sessile glands).

Description

Spiny shrub, stems variously prostrate, spreading, erect or scandent, (0.4–) 1–2 m tall; young stems green to brown, 4-angular, sparsely pubescent with short bristly unbranched hairs, increasing in density at and immediately below nodes, most dense on two opposite sides, can be slightly retrorse, strigose at nodes; older stems woody, up to 7 mm in diameter. *Axillary spines* beige-white, sessile or stalk to 2 mm long, 4-rayed, rays of similar length or 2 longer, straight, longest ray 11–22 (–29) mm long. *Leaves* on petioles 0.7–1.4 cm long; blade broadly elliptic to suborbicular or occasionally ovate, 29–56 × 22–39 mm (length: width ratio 1.2–1.7: 1), base cuneate to obtuse, margin entire, apex acute to rounded, sometimes with a minute apical spine 0.5–1 mm long, adaxial surface often glabrous, sometimes with short fine hairs along midrib and veins, abaxial surface with short fine ascending hairs, most dense along veins, hairs unbranched, margins and occasionally midrib strigose; lateral veins 3–4 per side, strongly ascending, these and midrib prominent abaxially and adaxially. *Inflorescences* terminal, subcapi-

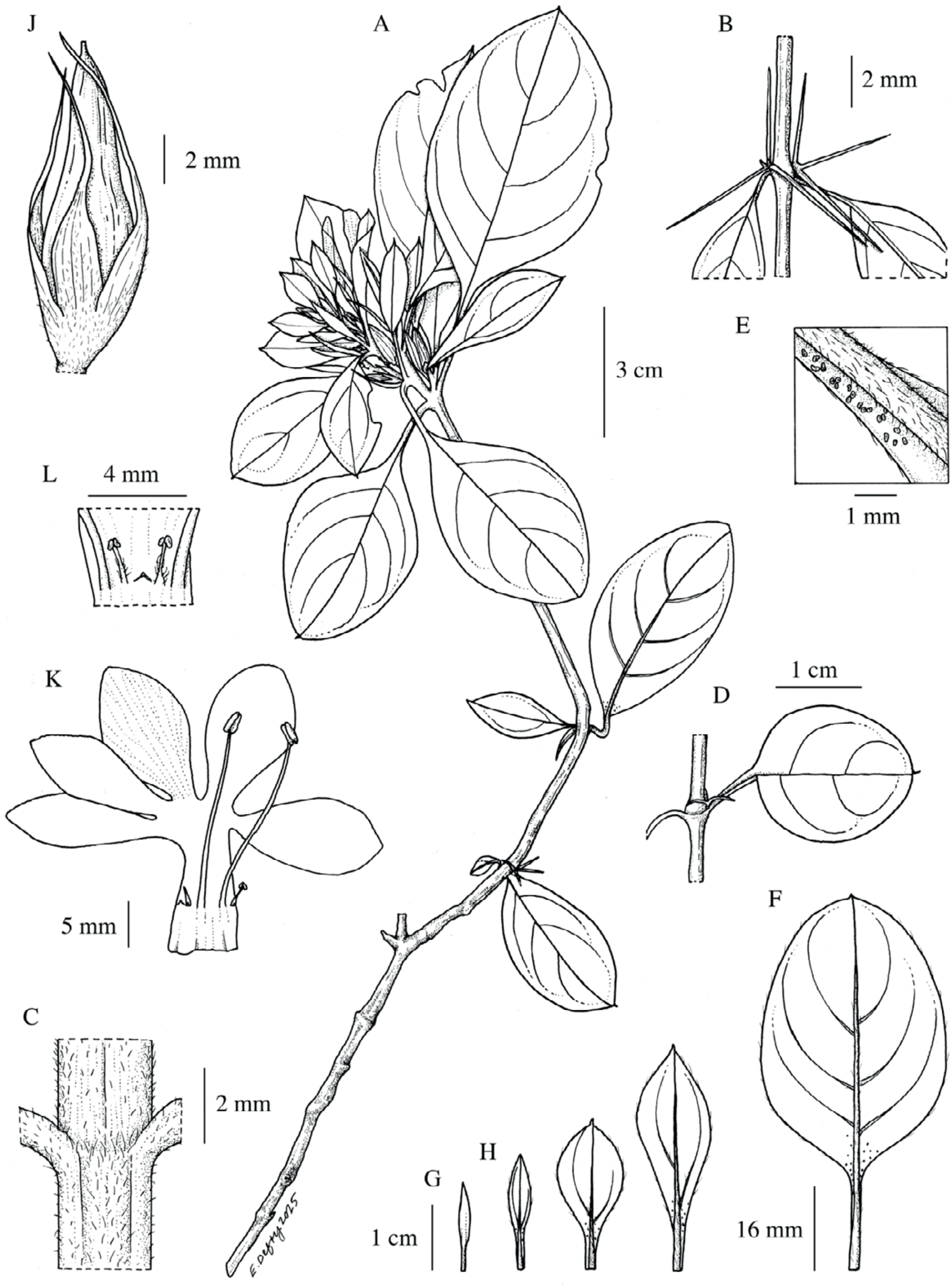

Figure 7. *Barleria sebsebei*. **A.** Habit, flowering branch. **B.** Stem node with proximal portions of leaves and with axillary spines. **C.** Young stem indumentum, at node. **D.** Leaf in situ, adaxial surface, with axillary spine. **E.** Leaf indumentum, base of abaxial surface with broad sessile glands. **F.** Proximal-most bract, abaxial surface. **G.** Bracteole. **H.** Bracts, variation in shape moving distally (l) to proximally (r), abaxial surfaces. **J.** Fruiting calyx with immature capsule. **K.** Dissected corolla with androecium, abaxial corolla lobe second from the right. **L.** Short lateral stamens and staminode. A, C, E–H, K–L. drawn from *M. G. Gilbert et al. 8257* (K); B drawn from *I. Friis et al. 14746* (K), D. drawn from *M. G. Gilbert & Sebsebe D. 8628* (K); J. drawn from *I. Friis et al. 10949* (K). Drawn by Ellie Defty.

tate to shortly spiciform, 2.1–4.3 cm long, each axil with a 3–7-flowered dichasial cyme when mature (distalmost axils can be 1-flowered); basal bracts leaf like, up to 8.2 × 4.4 mm, distal bracts green, lanceolate to obovate, 17–20 × 4.5–11 mm including spine tip 0.9–1.1 mm long; indumentum as on leaves but also with occasional short glandular hairs on abaxial surface or glabrous, and with conspicuous and ± numerous broad sessile glands proximally on abaxial surface; bracteoles green, linear-lanceolate, 14–26 × 1.5–2 mm, strigose along margin and with short fine hairs along midrib, conspicuous broad sessile glands numerous proximally; flowers shortly pedicellate, pedicel fused to the subtending bracteole. *Calyx* green to dark green in flower, turning pale green-white in fruit; anterior lobe lanceolate, ± 9.5 × 2 mm in flower including spine tip 3.2 mm long, apical spine can be bifid, extending to ± 13 × 2.9 mm in fruit including spine tip 5.5 mm long, external surface glabrous or with short ascending or appressed eglandular hairs concentrated proximally along midrib, internal surface glabrous; posterior lobe as anterior lobe but ± 10.3 × 2.7 mm in flower including apical spine ± 5 mm long, extending to ± 13.5 × 2.9 mm in fruit including apical spine ± 6.5 mm long; lateral lobes narrower, 9.2–10 × 1–1.2 mm in flower including apical spine 3.2–4.8 mm long, extending to 11.8–12 × 2 mm in fruit including apical spine 5–5.5 mm; midrib and parallel veins prominent abaxially and adaxially on all lobes when in fruit; anterior lobe lanceolate. *Corolla* bluish-purple, 30–37 mm long, glabrous externally; tube cylindrical, ± 13 mm long, ± 5.9 mm diameter at base, ± 4 mm at narrowest point; limb in weak “4+1” configuration; abaxial lobe offset by ± 1.5 mm, broadly obovate, ± 17.3 × 10 mm, apex rounded; lateral lobes oblanceolate, 17.5–17.8 × 8–10 mm, apices acute (ratio of abaxial: lateral lobe length ± 0.97–1: 1); adaxial lobes elliptic to obovate, 18–18.5 × 6.6–6.7 mm, apices acute. *Stamens* inserted 6.3–6.5 mm from base of corolla tube; filaments of long stamens 18–18.5 mm long; anthers ± 3.1 mm long; short lateral stamens with filaments ± 1.8 mm long, with flimsy subulate hairs, antherodes 0.5–0.7 mm long. *Ovary* not seen; style glabrous; stigma linear, 0.45–0.5 mm long. *Capsule* only seen in immature state, glabrous; seeds not seen.

Etymology

This species is named in honour of Professor Sebsebe Demissew, for his exceptional contributions to our knowledge of the Ethiopian and wider African flora and its conservation.

Distribution

This species is known from two small areas of the southeastern portion of Oromia regional state in southern Ethiopia (BA and SD floristic regions), specifically in the vicinity of Bidrē and to the south of Negele towards Melca Guba. Fig. 3.

Habitat and Ecology

This species occurs in mixed vegetation comprising *Senegalia*-*Commiphora* woodland often with *Combretum* and *Terminalia* spp. on rocky limestone escarpments and areas with clay-covered or red sandy soils. It is also associated with various *Euphorbia* spp. and *Kirkia* sp. These habitats can range from short, overgrazed grassland to dense thickets that include *Cadia*, *Carissa*, *Fagaropsis*, *Pistacia aethiopica* Kokwaro and *Psydrax* sp. Other associated woody plants include *Euclea*, *Grewia* and *Lannea* spp. This species has also been noted in areas with creeks and drainage lines, where vegetation is particularly rich. It occurs at elevations of 1250–1650 m.

Conservation status

This species has an area of occupancy (AOO) of 20 km^2 and an extent of occurrence (EOO) of 968 km^2. Despite its relatively large EOO, it is only known from six collecting localities in two small areas, the first in the vicinity of Bidrē and the second to the south of Negele towards Melca Guba. These are deemed to represent 2–3 threat-defined locations. The pastoral and agricultural activities that are widespread in this region, particularly at lower elevations, present a potential threat, with Google Earth imagery showing intense farming activity throughout its range. The collecting localities in the north of the range may also be impacted by settlement expansion and human activity from nearby Bidrē. Half of the collected specimens were found on foot slopes or plateaux, where the rocky ground may provide this species with some degree of protection from agricultural encroachment, but it appears that much of its habitat is nevertheless disturbed to some degree. The species is also likely to be experiencing some levels of habitat loss due to overgrazing, but further surveys are needed to assess the true extent of this threat. Given the combination of its restricted AOO and EOO, its few locations and ongoing agricultural pressures, this species is given a preliminary assessment of **Endangered** under criterion B: **EN B1ab(iii)+2ab(iii)**.

Taxonomic notes

Barleria sebsebei has previously been treated as a form of *B. quadrispina*, e.g., by Ensermu (2006) who did not comment on these distinctive plants, although in herbarium collections it has been provisionally identified as distinct from that species. It is a conspicuously more robust and usually considerably taller species (often ≥ 1 m) than *B. quadrispina* and the broad leaves, the bracts with numerous and conspicuous broad sessile glands towards the base and the relatively large corollas are together diagnostic. The robust stature of *Barleria sebsebei* and the presence of broad sessile glands on the abaxial surface of the bracts are similar to *B. ferox* from Harar region of northeast Ethiopia and, indeed, these two species cluster together in the PCA analysis (Figure 1) but they are easily separated by the spine, leaf and calyx characters listed in the Diagnosis above.

The range of *Barleria sebsebei* is closely similar to that of *B. negeleensis*, but the two species are very different morphologically in a range of characters, for example *B. negeleensis* is a short, stout perennial ≤ 40 cm tall with narrowly oblong or oblong-elliptic leaves with conspicuously spinose apices, ovate to oblong-elliptic bracts in the proximal portion of the inflorescence, and a ± densely glandular and eglandular calyx indumentum These two species are unlikely to be confused.

For phytogeographic affinities of this species, see note under *Barleria filtuensis*.

Additional specimens examined

ETHIOPIA. Bale, edge of escarpment 6 km from Biddre [Bidrē] on road to Dello Mena [Delo Menna] (Maslo), 05°51'N, 39°36'E, 2 June 1988 (fl.), *M. G. Gilbert & Sebsebe D. 8628* (ETH!, K! [K001295216], UPS!); Bale, 32 km from Genale river bridge along the track from Bitata to Vidre [Bidrē] and Dalo Manna [Delo Menna] (83 km from Negelle [Negele]), 29 May 1996 (fl.), *Ensermu K. & Dessalegn D. 3778* (ETH!); Sidamo, 42 km from Negelle [Negele] along the road to Malka Guba [Melka Guba], 30 May 1996 (fl.), *Ensermu K. & Dessalegn D. 3787* (ETH!); ca. 48 km from Negelle [Negele], along the road towards Melca Guba [Melka Guba], Hudat, Wachile and Arero, 05°06'N, 39°32'E, 13 Dec. 2002 (fl.), *I. Friis et al. 10949* (K! [K001295215]); Oromya [Oromia] Region, Sidamo, 28 km on Melka Guba Road from turn off from Filtu road, 05°06'N, 39°34'E, 2 Oct. 2003 (fl.), *S. Bidgood et al. 4961* (ETH, K! [K001295241]); Biddre [Bidrē] to Sidambale Bridge, 6 km from Biddre [Bidrē], 05°55'N, 39°35.50'E, 3 Dec. 2012 (fl.), *I. Friis et al. 14746* (K! [K001295212]).

7. *Barleria ferox* Ensermu & I.Darbysh. in Kew Bull. 73(1)-1: 13. 2018.

Type: Ethiopia, Harar Region, near Galacia, 10 Nov. 1963 (fl., fr.), *W. Burger 3349* (holotype ETH!; isotypes FT, K! [K001290016]).

(=) *Barleria* sp. [= *Amare G. D-10*] *sensu* Ensermu in Fl. Ethiopia & Eritrea 6: 415. 2006.

For a full description and illustration, see Ensermu and Darbyshire (2018: 13, Fig. 5).

Distribution

This species is restricted to Oromia regional state (HA floristic region) in eastern Ethiopia. Fig. 3.

Habitat and Ecology

Only very limited information is available on the ecology of this species; on the type specimen it was recorded from open limestone slopes with shrubs and no trees, whilst *Amare Getahun (D-10)* recorded it from a "dry area"; ca. 1400–1600 m elevation.

Conservation status

This highly range-restricted species, with an EOO of only 1,348 km^2 based on current evidence, is assessed as **Endangered** under criterion B on the IUCN Red List: **EN B1ab(iii)** (Darbyshire et al. 2023). It is threatened by habitat loss and degradation due to the expansion of human residential infrastructure and the expansion of agriculture in parts of its range.

Taxonomic notes

See notes to *Barleria sebsebei* on how these two allopatric species differ. For phytogeographic affinities of this species, see note under *Barleria filtuensis*.

Additional specimens examined

ETHIOPIA. Harar region, Jijiga Road, 15 Sept. 1958 (fl.), *Amare G. D-10* (EA!, K! [K001290014]); 90 km S of Harar on road S of Midaga, 14 Oct. 1962 (fl., fr.), *W. Burger 2190* (ETH!, FT!, K! [K001290015]).

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STATEMENT OF INTERESTS

The authors declare no conflicts of interest or competing interests.

REFERENCES

Bachman S, Moat J, Hill AW, de la Torre J, Scott B. 2011. Supporting red list threat assessments with GeoCAT: Geospatial conservation assessment tool. ZooKeys. 150: 117–126. https://doi.org/10.3897/zookeys.150.2109

CEPF. 2025. Critical Ecosystem Partnership Fund. Horn of Africa Biodiversity Hotspot, [accessed 2025 Feb 25]. Available from: https://www.cepf.net/our-work/biodiversity-hotspots/horn-africa

Comito R, Darbyshire I, Kiel C, McDade L, Fisher AE. 2022. A RADseq phylogeny of *Barleria* (Acanthaceae) resolves fine-scale relationships. Molecular Phylogenetics and Evolution. 169: 107428. https://doi.org/10.1016/j.ympev.2022.107428

Darbyshire I, Vollesen K, Ensermu K. 2010. Acanthaceae (part II). In: Beentje H. (Ed.), Flora of Tropical East Africa. London: Royal Botanic Gardens, Kew.

Darbyshire I, Fisher AE, Kiel CA, McDade LA. 2019. Phylogenetic relationships among species of *Barleria* (Acanthaceae, Lamiales): Molecular data reveal complex patterns of morphological evolution and support a revised classification. Taxon. 68: 92–111. https://doi.org/10.1002/tax.12029

Darbyshire I, Roberts A. 2023. *Barleria negeleensis*. IUCN Red List Threat Species. 2023:e.T219403827A219405363. https://doi.org/10.2305/IUCN.UK.2023-1.RLTS.T219403827A219405363.en

Darbyshire I, Roberts A, Sebsebe D. 2023. *Barleria ferox*. IUCN Red List Threat Species. 2023:e.T219403659A219405343. https://doi.org/10.2305/IUCN.UK.2023-1.RLTS.T219403659A219405343.en

Defty E, Darbyshire I. 2024. New taxa of *Barleria* sect. *Prionitis* (Acanthaceae) from the Horn of Africa biodiversity hotspot in Somalia. Webbia. 79:19–29. https://doi.org/10.36253/jopt-15729

Ensermu K. 2006. Acanthaceae. In: Hedberg I, Ensermu K, Edwards S, Sebsebe D, Persson E. (Eds.), Flora of Ethiopia and Eritrea. Vol. 5. Addis Ababa: The National Herbarium, Addis Ababa University; Uppsala: The Department of Systematic Botany, Uppsala University. Pp. 345–495.

Ensermu K, Darbyshire I. 2018. Six new species of *Barleria* L. (Acanthaceae) from northeast tropical Africa. Kew Bulletin 73(1):1. https://doi.org/10.1007/s12225-017-9725-2

Friis I, Sebsebe D, van Breugel P. 2010. Atlas of the Potential Vegetation of Ethiopia. Biologiske Skrifter. 58: 1–307.

Friis I, van Breugel P, Weber O, Sebsebe D. 2022. The Western Woodlands of Ethiopia - A study of the woody vegetation and flora between the Ethiopian Highlands and the lowlands of the Nile Valley in the Sudan and South Sudan. Scientia Danica. Series B, Biologica 9: 1–521.

Hanny L, Hoban G, Lockyear O, Belcher A, Svahnström VJ, Darbyshire I. 2024. Additions to and revisions of the endemic and near-endemic Acanthaceae of Ethiopia. Webbia. 79: 201–225. https://doi.org/10.36253/jopt-16074

Hedberg I, Friis I, Persson E. (Eds.) 2009. Flora of Ethiopia and Eritrea. Vol. 8: General Part and Index to Vols 1–7. Addis Ababa: The National Herbarium, Addis Ababa University; Uppsala: The Department of Systematic Botany, Uppsala University.

Hedrén M. 2006a. *Barleria*. In: Thulin M. (Ed.), Flora of Somalia. Vol. 3. London: Royal Botanic Gardens, Kew. Pp. 427–442.

Hedrén M. 2006b. New species and combinations in Acanthaceae from Somalia. Willdenowia. 36: 751–759. https://doi.org/10.3372/wi.36.36210

IUCN. 2012. IUCN Red List Categories and Criteria: Version 3.1. Second edition. Gland & Cambridge: IUCN Species Survival Commission. https://portals.iucn.org/library/node/10315

IUCN. 2024. Guidelines for the application of IUCN Red List of Ecosystems Categories and Criteria, Version 16. Prepared by the Standards and Petitions Committee, [accessed 2025 May 01]. https://www.iucnredlist.org/resources/redlistguidelines

Lindau G. 1896. Contribuzioni alla conoscenza della flora dell’Africa orientale. Acanthaceae somalenses a DD. L. Bricchetti-Robecchi et Dr. Riva in Harrar et in Somalia lectae. Annuario del Reale Istituto Botanico di Roma. 6: 67–83.

Lovett JC, Friis I. 1996. Patterns of endemism in the woody flora of north-east and east Africa. In: Van der Maesen LJG, van der Burgt XM, van Medenbach de Rooy JM. (Eds.), The Biodiversity of African Plants: Proceedings of the 14th AETFAT Congress 22–27 August 1994, Wageningen, The Netherlands. Dordrecht: Kluwer Academic Publishers. Pp. 582–601.

Polhill D. 1988. Flora of Tropical East Africa. Index of Collecting Localities. London: Royal Botanic Gardens, Kew.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rendle RB. 1896. Dr. Donaldson Smith's Acanthaceae. Journal of Botany 34: 395–398.

Thulin M. (Ed.) 1993. Flora of Somalia. Vol. 1: Pteridophyta; Gymnospermae; Angiospermae (Annonaceae–Fabaceae). London: Royal Botanic Gardens, Kew.

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A taxonomic synopsis of *Heterotis* (Melastomataceae), including *H. kupensis* sp. nov., a threatened species endemic to Mt Kupe, Cameroon

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Abstract. We provide a synopsis of the African genus *Heterotis* (Melastomataceae), recognising seven species and including the description of a species new to science *Heterotis kupensis* Sv. & Cheek (Melastomataceae) known only from Mt Kupe in the South West Region of Cameroon. It differs from all other members of the genus by its tardily caducous, oblong calyx lobes; hastate pedoconnectives on the antesepalous stamens with transversely ellipsoid ventral appendages; the hypanthium covered by hairs with thickened bases as well as filiform appendages on the upper half only; sessile leaf-blades and the yellow centre to the flower. In addition, we select lectotypes for *H. prostrata* (Thonn.) Benth. and *H. fruticosa* (Brenan) Ver.-Lib. & G.Kadereit, a second step lectotype for *H. buettneriana* (Cogn.) Jacq.-Fél. and designate the new name *H. welwitschii* (Cogn.) Sv. & Cheek to replace the illegitimate *H. cogniauxiana* (A.Fern. & R.Fern.) Ver.-Lib. & G.Kadereit. Morphological species delimitation between *H. decumbens*, *H. prostrata*, and *H. rotundifolia* is difficult and intermediate specimens are common. *Heterotis rotundifolia* is widely reported as naturalised and invasive, however many occurrences from outside of mainland Africa actually represent *H. prostrata* or have intermediate morphology. *Heterotis decumbens* has been introduced and naturalised in Madagascar and the Mascarene Islands. Distribution, habitat, phenology, taxonomic notes, and preliminary conservation assessments following IUCN Red List criteria are presented along with a key to the species.

Keywords: aliens, conservation, endemic, *Heterotis*, invasives, Melastomataceae.

INTRODUCTION

Melastomateae are a morphologically diverse and species-rich pantropical tribe of Melastomataceae characterised by cochleate seeds with tubercles, a crown of bristles on the apex of the ovary and staminal pedoconnectives with bifurcated ventral appendages (Veranso-Libalah et al. 2022). The Melastomateae are the most species-rich melastome tribe in Africa, consisting of

24 genera and about 143 species (Veranso-Libalah et al. 2020; Chen et al. 2025). Delimitation of genera in African Melastomateae has historically been challenging due to extensive diversity and variation in a multitude of morphological characters, exacerbated by the apparent prevalence of evolutionarily labile traits within the tribe e.g. stamen isomorphy vs dimorphy. The genus *Heterotis* Benth. was first recognised by Bentham (1849) who proposed four sections *Heterotis* Benth., *Cyclostemma* Benth., *Leiocalyx* Benth., and *Wedeliopsis* Benth. In his treatment, Bentham (1849) defined *Heterotis* on the basis of its persistent, laciniate calyces with setose appendages on the hypanthium, dimorphic anthers, and loculicidal capsules. Triana (1872) transferred all of the species in sections *Leiocalyx* and *Wedeliopsis* to *Tristemma* Juss., and sections *Heterotis* and *Cyclostemma* were subsumed into a broadly defined *Dissotis* as sect. *Heterotis*, elevated to subg. *Heterotis* (Benth.) A.Fern. & R.Fern by Fernandes and Fernandes (1969). Jacques-Félix (1981) resurrected *Heterotis* at the rank of genus, recognising that staminal dimorphism, the defining character of Triana's (1872) concept of *Dissotis*, is an unreliable trait for generic classification. He defined three sections within *Heterotis*: sect. *Heterotis*, sect. *Argyrella* (Naudin) Jacq.-Fél. and sect. *Cyclostemma*.

Recently, the African Melastomateae have undergone revision in light of phylogenetic study, resulting in an updated classification of 24 monophyletic genera each diagnosed by combinations of morphological characters and supported by generic keys (Veranso-Libalah et al. 2017; Veranso-Libalah et al. 2020; Chen et al. 2025). Many accepted genera including *Heterotis* were found to be polyphyletic as previously circumscribed. Traits which have previously been used to define genera in this tribe such as flower merosity, habit, and isomorphic vs. dimorphic stamens are now, in a phylogenetic framework, recognised to have been gained and lost many times. As a result, *Heterotis* was recircumscribed, resulting in a more narrowly defined, monophyletic genus, consisting only of section *Heterotis* sensu Jacques-Félix (1981).

Veranso-Libalah et al. (2017) distinguished *Heterotis* morphologically from other African Melastomateae on the basis of the following combination of characters: decumbent herbs, leaves orbicular to ovate-lanceolate, hypanthium with stalked emergences, flowers large, 5-merous, calyx-lobes persistent, apex of intersepalar appendages with stellate emergences, and seeds cochleate and visibly arillate. Six species were recognised in the genus *Heterotis*, three of which are restricted to the Guinean-Congolian region (*H. fruticosa* (Brenan) Ver.-Lib. & G.Kadereit, *H. cogniauxiana* (A.Fern. & R.Fern.) Ver.-Lib. & G.Kadereit *nom. illegit.*, and *H. buettneriana* (Cogn.) Jacq.-Fél.), whereas the remaining three are more widely distributed in tropical Africa (*H. decumbens* (P.Beauv.) Jacq.-Fél., *H. prostrata* (Thonn.) Benth., and *H. rotundifolia* (Sm.) Jacq.-Fél.). Within species of the genus, several characters exhibit extensive variation, including some that were previously used for species delimitation, such as hypanthium indumentum, leaf shape, and habit. As a result, there has been confusion in distinguishing between species. Previous treatments have considered *H. prostrata* as a synonym (Wickens 1975) or variety of *H. rotundifolia* (Jacques-Félix 1971) and *H. rotundifolia* as indistinguishable from *H. decumbens* (Gilbert 1995). *Heterotis fruticosa* was originally described as a variety of *H. rotundifolia* before being elevated to species rank (Brenan 1950; Keay 1953). In the most recent species-level treatment of the genus, Jacques-Félix (1981; 1995) recognised six species but suggested that they are closely related, and that the widespread and particularly problematic and variable *H. rotundifolia*, *H. prostrata* and *H. decumbens* could represent a species complex.

Until now, no new species had been added to *Heterotis* s.s. since the description of *H. fruticosa* (as *Dissotis rotundifolia* var. *fruticosa*) (Brenan 1950). During fieldwork in 1995 on Mt Kupe in Cameroon, a distinctive species of Melastomateae was collected from grassland at the summit. It was first recognised as a provisionally new taxon (*Dissotis sp. 1*) in a checklist for Mt Kupe (Cheek et al. 2004). The generic keys and descriptions in Veranso-Libalah et al. (2017; 2020) support this species' placement in the genus *Heterotis* based on the presence of stalked stellate emergences on the hypanthium, intersepalar appendages with stellate hairs at the apex, cymose inflorescences, and large, 5-merous flowers.

Here, we provide a taxonomic synopsis of the seven species presently recognised in the genus *Heterotis* (Figure 1), including description of a previously unnamed species from Cameroon. We also designate a new name to replace the illegitimate *H. cogniauxiana*, lectotypes for *H. prostrata* and *H. fruticosa*, and a second step lectotype for *H. buettneriana*. We further present preliminary conservation assessments and a key to all the species in the genus.

MATERIALS AND METHODS

This study is predominantly based on herbarium specimens held at K, and in some cases images from other herbaria including BM, BR, C, COI, FHI, G, G-DC, LINN, LISU, MO, NY, P, US, and WAG. The description of the new species is based on seven duplicates of the type, which comprise all of the known material for this taxon at present. Material of the new species was

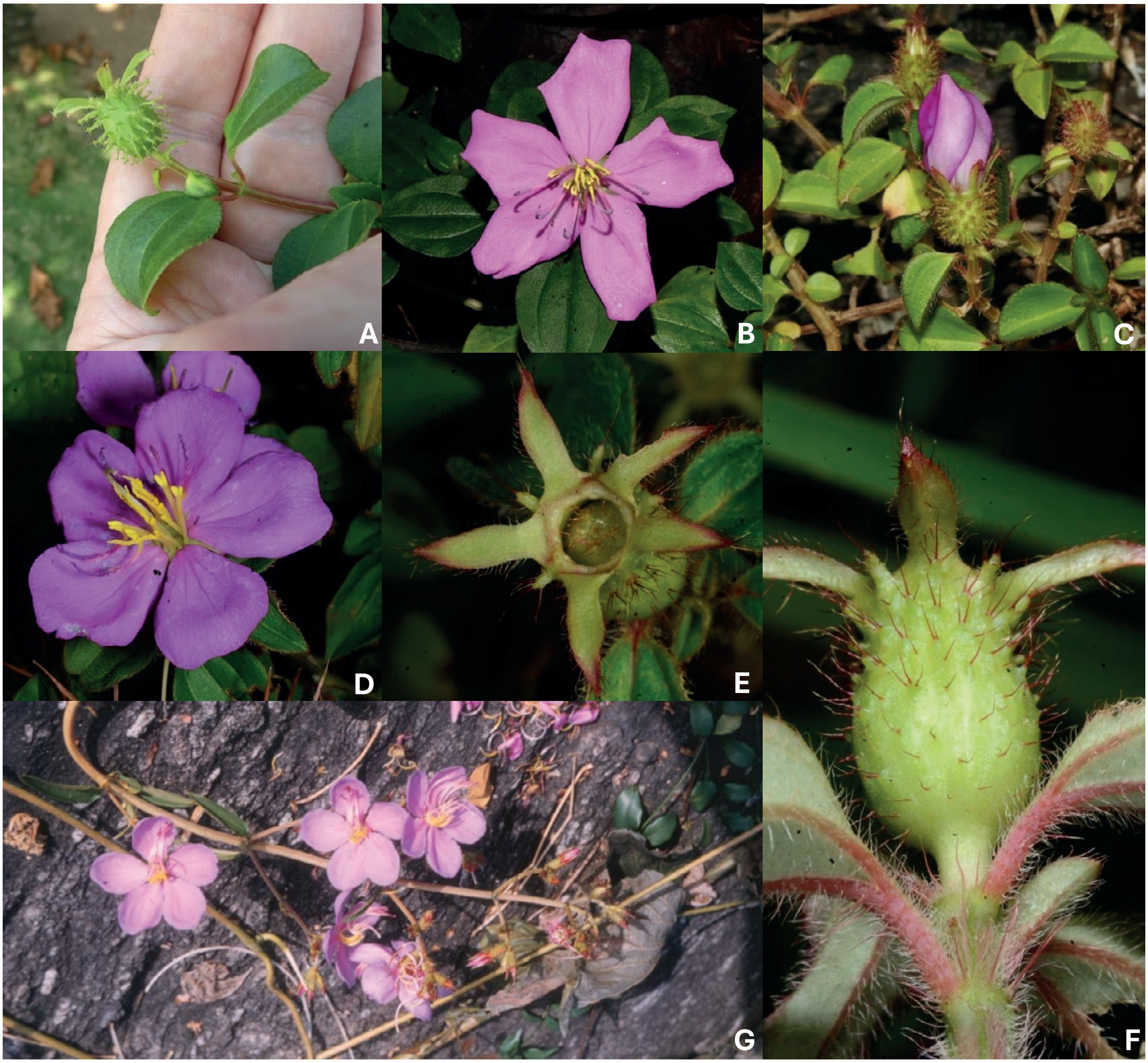

Figure 1. Representatives of the genus *Heterotis*. **A.** *H. prostrata* hypanthium and calyx; **B-C.** *H. rotundifolia* flower (B) and plant (C); **D-F.** *H. decumbens* flower (D), calyx (E) and hypanthium (F); **G.** *H. fruticosa*. Photos: A. Carel Jongkind; B. Vida J. Svahnström; C. James Bailey; D-F. Ehoarn Bidault; G. RBG, Kew.

compared morphologically with material of all other species of *Heterotis* held at K. All of the specimens seen by the authors are indicated with an exclamation mark ("!") whereas specimens for which we examined images are marked "image". Images (e.g. via gbif.org) were usually of insufficient resolution to enable or confirm identifications. There was insufficient time during the project (2024 to 2025) for the principal author (VS) to obtain material on loan to K for this study and no funds available for her for herbarium visits in relation to this work. Herbarium material was examined using a Leica M165C dissecting binocular microscope. The drawing was made using a Leica Wild M8 dissecting binocular microscope fitted with an eyepiece graticule measuring in units of 0.025 mm at maximum magnification with a Leica 308700 camera lucida attachment. Type specimens are not given for all homotypic names in synonymy. The conservation assessment follows the categories and criteria of the International Union for the Conservation of Nature (IUCN 2012) and the guidelines for their use (IUCN 2024).

TAXONOMIC TREATMENT

Heterotis Benth., Niger Fl.: 347. 1849.

Type species: *Heterotis rotundifolia* (Sm.) Jacq.-Fél., Adansonia, n.s., 20: 417. 1981.

Note. Two species in the present circumscription of *Heterotis* Benth. were included in the protologue of the genus: *Heterotis prostrata* (Thonn.) Benth. and *H. rotundifolia* (Sm.) Jacq.-Fél. as *Osbeckia rotundifolia* Sm., which was treated as a synonym of *H. plumosa* Benth. Fernandes and Fernandes (1969) designated *Dissotis rotundifolia* (Sm.) Triana as the type species of *Dissotis* sect. *Heterotis*, prior to its resurrection as the genus *Heterotis*. The type species of *Heterotis* is therefore *H. rotundifolia*: Index Nominum Genericorum (Farr et al. 1996) appears to have overlooked the work of Fernandes and Fernandes (1969) in error, listing the type of *Heterotis* as non designatus.

Key to the species

1. Stems erect, not rooting at the nodes; subshrubs.................2

1. Stems prostrate, rooting along their length; decumbent herbs 4

2. Calyx-lobes tardily caducous, oblong; antesepalous stamens with pedoconnectives hastate, ventral appendages transversely ellipsoid. Cameroon...........................**1. *H. kupensis***

2. Calyx-lobes persistent, linear-ovate; antesepalous stamens with pedoconnectives linear, ventral appendages bilobed.3

3. Leaves elliptic-oblong, to 3 cm wide; length: breadth 2:1, sepals persisting in fruit, flat. W.Angola ...**2. *H. welwitschii***

3. Leaves narrowly lanceolate-elliptic, to 1.5 cm wide; length: breadth 3:1, sepals rapidly shrivelling in fruit, W. Nigeria .. ..**3. *H. fruticosa***

4. Stamens isomorphic; apex of calyx-lobes with excurrent emergence bearing a cluster of stellate hairs ....**4. *H. buettneriana***

4. Stamens dimorphic; apex of calyx-lobes with or without excurrent emergence..5

5. Hypanthium with simple hairs or unisetulous bristles only, without stalked, stellate emergences..........**5. *H. decumbens***

5. Hypanthium with stalked, stellate emergences.....................6

6. Apex of calyx-lobes with excurrent emergence bearing a cluster of stellate hairs ....**6. *H. prostrata***

6. Apex of calyx-lobes with cluster of stellate hairs, not excurrent...**7. *H. rotundifolia***

1. *Heterotis kupensis* Sv. & Cheek, **sp. nov.**

Type: Cameroon, S.W. Province, NE side of Mt Kupe, Peak No. 2, 1900 m elev., fl. 11 Jan. 1995, *Sidwell K.* 428 with Cheek, Gosline, Okah, Etuge, Oyugi (holotype K; isotypes BR, CAS, K, SCA, YA). (Figures 2, 3, 4).

Dissotis sp. 1 Cheek & Woodgyer in Cheek et al. (2004: 335 & plate 9F).

Diagnosis

Heterotis kupensis differs from all other members of the genus by its tardily caducous, oblong calyx lobes and hastate pedoconnectives on the antesepalous stamens with transversely ellipsoid ventral appendages. All other species of *Heterotis* have antesepalous stamens lacking a hastate base and having bilobed ventral appendages. Additionally, the new species is unique in that the hypanthium is covered by hairs with thickened bases as well as filiform appendages on the upper half only, whereas the hypanthium is uniformly covered with filiform appendages in all other species, except for *H. decumbens* which has only simple hairs on the hypanthium. The leaves of *H. kupensis* appear subsessile with short (< 3.5 mm) petioles, whereas most specimens of the remaining six species of *Heterotis* are distinctly petiolate. *Heterotis kupensis* is also the only species in the genus which has a corolla with a yellow centre; the other species have a uniformly pink (occasionally white) corolla.

Description

Erect herb 55–75 cm tall, with multiple stems from the base, stems ascending, woody at the base, unbranched their entire length, or sparingly and shortly branched in the distal half, sometimes rooting at nodes, stems with internodes 3.2–6.5 cm long, becoming shorter distally, covered with spreading hairs (1.0–)1.5–4.5(–5.5) mm long, scattered on internodes and in a dense ring at nodes. *Leaves* simple, opposite, elliptic or elliptic-ovate, drying brown, leaves (0.8–)2.4–3.6 x (0.5–)1.2–1.9 cm, decreasing in size up the stem, each leaf with apex acute, base rounded, margins entire to minutely crenulate with appressed bristle bases along entire length, bristles 1.5 –3.0 mm; midnerve and two pairs of lateral nerves impressed on adaxial surface of lamina, prominent on abaxial surface, lateral nerves diverging from the midnerve at the base of the blade, curvilinear, outer pair of lateral nerves terminating at leaf margin 3/4 of the length of the lamina, inner pair of lateral nerves meeting or nearly meeting the midnerve at the leaf apex, transverse veins only faintly visible, forming weak arches. Adaxial surface of lamina covered (20% cover) with simple antrorse strigose hairs, more or less sigmoid, 1.0–4.5 mm with a swollen botuliform base appressed ca. 0.5 mm long, the distal part fine, bristlelike, hairs becoming shorter towards the apex of lamina, abaxial surface (10% cover) with simple antrorse, slightly appressed hairs, with less pronounced swollen bases than hairs on adaxial surface, 1.0–3.8 mm long, hairs sparse on abaxial lamina surface, denser on the principal veins; petiole terete 2.0–3.5 mm long, hairs as lamina. *Inflorescence* terminal, cymose, (1–)4–5(–6) flowered, or with 1–2 flowers in upper axils, flowers 5-merous, pedicels 2–4 mm long. *Bracts* caducous, falling at anthesis, two pairs per flower, the outer pair 3.0–4.5 x 2.0 mm drying tan, ovate, glabrous except for ciliate margins with cilia 1.0-3.5 mm long, inserted 1.5–2.0 mm above the most distal leaf node, inner pair inserted 2.0 mm above the outer pair and 1.0 mm below the flower, drying purple, ovate, 2.0–2.7 x 1.5–2.5 mm, glabrous except for ciliate margins with cilia 0.8–1.3 mm long. *Hypanthium* campanulate 5.0–9.5 x 4.3–6.0 mm, densely covered with persistent white hairs 2.5–3.5 mm long with swollen bases, penicillate appendages on the upper ½ of hypanthium 0.3–0.9 x 0.2–0.4 mm with a tuft of 1–4 white hairs, upper ½ of hypanthium also with purple, filiform appendages 1.2–2.0 x 0.2–0.3 mm, stellate with many white hairs at apex; intersepalar appendages similar in form and colour to the filiform hypanthial appendages but caducous, larger, 2.0–2.9 x 0.2–0.4(–0.8) mm. *Calyx* green drying purple, sepals oblong, 5.0–7.5 x 2.5–3.5 mm, tardily caducous, falling after anthesis, margins ciliate with cilia (0.1–)0.5–1.0(–2.0) mm long, glabrous on the inside, with very few short hairs near base on the outside 0.4–1.4 mm long, and a thickened stellate cluster of many white hairs each 1.0–4.0 mm long at the apex. *Corolla* pale pink, centre yellow with a dark pink edge, petals five, obovate, 2.0–2.5 x 2.0–2.5 cm, glabrous except for ciliate margins with cilia 0.2–0.5(–1.5) mm long. *Stamens* ten, yellow with pink anthers opening by an introrse pore, dimorphic, antesepalous stamens five, filament 3.0–4.0 x 0.5–1.0 mm, pedoconnective hastate, 3.5–4.5 mm long, 1.0–1.5 mm wide at base, tapering at the apex, the proximal arms approximately triangular, diverging from the truncate base of the connective and each other by c. 180°, ventral appendage pair swellings transversely ellipsoid, 0.5–0.7 mm collateral at the connective base, anther falcate, 4.5–5.0 x 0.5–1.0 mm, antepetalous stamens five, filaments 2.5–3.5 x 0.5–1.0 mm, pedoconnective not developed, ventral appendages spreading, each ovoid 0.2–0.3 mm long, diverging from each other by 90°, anther 2.5–3.0 x 0.5–1.0 mm, erect. *Ovary* ellipsoid ca. 2.0 x 1.5 mm, sparsely covered in white hairs 0.5–1.0 mm long, with a ring of five appendages at apex surrounding the style, persistent in fruit, appendages comprised of 5-7 erect bifurcating bristles each 1.0 –1.5 mm long. *Style* ca. 15 mm long, glabrous, curved, stigma truncate. *Fruit* not seen.

Etymology

The species is named for Cameroon's Mt Kupe where it appears to be endemic. Other species endemic to and named for Mt Kupe include *Memecylon kupeanum* R.D. Stone *et al.* (Melastomataceae, Stone et al. 2008), *Afrothismia kupensis* Cheek (Afrothismiaceae, Cheek et al. 2019; 2024) and *Kupeantha kupensis* Cheek & Sonké (Rubiaceae, Cheek et al. 2018).

Phenology

Collected in flower in January.

Distribution and habitat

CAMEROON: South West Region, known only from the type collection made at the summit of Mount Kupe (Fig. 4). Montane grassland with *Adenocarpus mannii* and *Pentas sp.*, elevation *c.* 1900 m.

Conservation status

This species is known only from montane grassland at the summit of one of the peaks of Mt Kupe. The area of grassland at the peak is less than 1 km^2, and as such the extent of occurrence (EOO) and area of occupancy (AOO) are both calculated as 4 km^2 (using 2 km x 2 km grid cells, see IUCN guidelines), well below the thresholds for threatened categories under subcriteria B1 and B2. There are several other peaks on Mt Kupe with grassland areas at the summit; these have been explored by botanists and this species has not been found at any other localities. However, steep, inaccessible areas on these peaks have not been thoroughly surveyed (Cheek et al. 2004) and this species may occur on one or more peaks hitherto undetected. Even if this species occurs on these peaks, or in other areas of montane grassland adjacent to Mt Kupe, it is highly likely that the true AOO falls below the threshold for a threatened category, considering the small area of these summit grasslands. Moreover, extensive surveys in other upland areas of the Cameroon Highlands have been carried out but this species has so far been found in none of these (Cheek et al. 1996; Cable and Cheek 1998; Cheek et al. 2000; Maisels et al. 2000; Chapman and Chapman 2001; Cheek et al. 2004; Harvey et al. 2004; Cheek et al. 2006; Cheek et al. 2010; Harvey et al. 2010; Cheek et al. 2011). While the population size has not been assessed, and although this species was reported as common at its only known site,

Figure 2. *Heterotis kupensis*. **A.** habit (open flower from photo); **B.** leaf, adaxial surface; **C.** leaf, abaxial surface; **D.** hair, from leaf lamina, proximal part, adaxial surface; **E.** hair, from leaf midrib, abaxial surface; **F.** hair, from leaf lamina, abaxial surface; **G.** margin of leaf with 2 hair types, abaxial surface; **H.** stem indumentum; **I.** hypanthial ornamentation (flower bud); **J.** hypanthium (hairs omitted) part opened to show ovary apex and stamens, all but one petal removed; **K.** antepetalous (short) stamen, ventral face; **L.** as K, dorsal face; **M.** antesepalous (large) stamen, ventral face; **N.** as M, dorsal face; **O.** detail of M (pore at anther apex). A-O. all from Sidwell 428. Drawn by Andrew Brown.

Figure 3. Flower of *Heterotis kupensis* (*Sidwell* 428) Photo: Martin Cheek.

it is likely that less than 1,000 individuals occur there given the extremely small area of potentially suitable habitat. There are no known threats to this species at its type locality, and human encroachment does not currently extend beyond ca. 1,100 m elevation on Mt Kupe apart from on the eastern slopes. There is a potential future threat of fire, however no evidence of human-set fires has been detected on any of the peaks at Mt Kupe (Cheek et al. 2004). Given the likelihood that this species has an extremely small population size of less than 1,000 individuals, it is preliminarily assessed as Vulnerable D1.

Notes

Each of the three peaks of Mt Kupe have small areas of montane grassland with similar plant assemblages (Cheek et al. 2004), yet *H. kupensis* has only been collected from one of these, where it was recorded as being locally common. These areas of montane grassland are considered to be inselberg caps of their respective peaks (Cheek et al. 2004). Two other species of *Heterotis* (*H. fruticosa* and *H. cogniauxiana*) occur on inselbergs in Nigera and Angola respectively. These are also the only other species in the genus which consistently exhibit an upright, woody growth habit, whereas the remaining species are typically decumbent herbs that root at the nodes. The duplicates of the type specimen are believed to be from more than one individual in the same population by the second author, who was present at the collection. It is possible that this species might also occur in Bandoumkassa (Veranso Libalah pers. comm. to Cheek, 2025), however, until verified we consider this species to be endemic to Mt Kupe.

2. *Heterotis welwitschii* (Cogn.) Sv. & Cheek, **nom. nov.**

Bas.: *Osbeckia welwitschii* Cogn. in A.L.P.P. de Candolle & A.C.P. de Candolle, Monogr. Phan. 7: 333. 1891.

Type: Angola, Pungo Andongo, rio Cuanza, pr. de Sansamanda, *Welwitsch 907* (holotype G-DC barcode G00319429! image; isotypes: BM barcode BM000902297! image, COI barcode COI00005417! image, K barcode K000313363!, LISU barcode LISU209417, P barcode P000412573! image).

(=) *Dissotis cogniauxiana* A.Fern. & R.Fern., Bol. Soc. Brot., sér. 2, 28 : 67. 1954 (non *Dissotis welwitschii* Cogn. (Cogniaux 1891: 371).

(≡) *Heterotis cogniauxiana* (A.Fern & R.Fern.) Ver.-Lib. & G.Kadereit, Taxon 66 : 609. 2017. *nom. illegit.*, **synon. nov.**

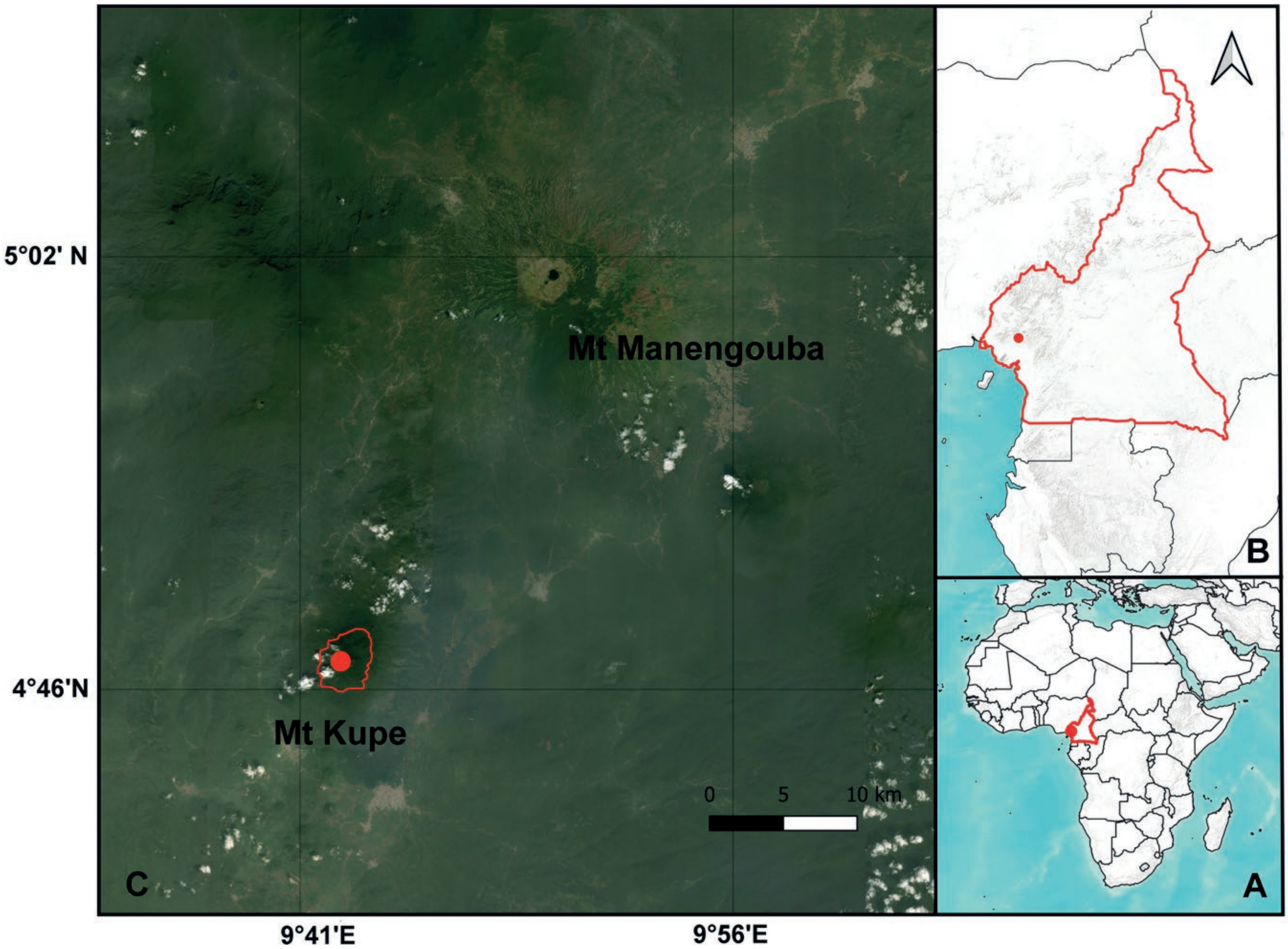

Figure 4. Global distribution map of *Heterotis kupensis*.

Etymology

Named for the Austrian botanical collector Friedrich Welwitsch (1806–1872), who collected the type material.

Phenology

Collected in flower between October–March, and in fruit January–March.

Distribution and habitat

Angola. Growing among rocks on the banks of streams in rocky deciduous woodland, 1,110–1,300 m elev.

Conservation status

Heterotis welwitschii is endemic to the Angolan highlands. Based on herbarium specimens, this species has a minimum EOO of 10,080 km^2, below the threshold for the Vulnerable category. *Plants of Angola* (Figueiredo and Smith 2008) lists this species from four provinces: Huila, Namibe, Malange, and Cuanza Norte. It is only represented from a single collecting locality in each of these provinces corresponding to four widely separated locations. However, it is likely that it is more widespread than can be inferred from specimen records due to low botanical collection effort across much of its large range, which extends from the northern to southern Angolan highlands. It is likely undergoing a continuing decline in the area, extent, and suitability of habitat at three of its known localities which are near towns (e.g. Bibala) or in areas which have been extensively converted for agriculture. However, there are large areas of potentially suitable habitat within its extensive range and the most recent collection is from Mt Tchivira, where the native vegetation is intact. This species could potentially qualify as Vulnerable if it is in fact known from fewer than ten locations undergoing a continuing decline, or it may be Least Concern if found to be more widespread. Thus, given the uncertainty, this species is preliminarily assessed as Near Threatened B1b(iii).

Notes

Osbeckia welwitschii Cogn. typified by *Welwitsch 907* was published in the same work as *Dissotis welwitschii* Cogn. [º *Eleotis welwitschii* (Cogn.) Ver.-Lib. & R.D.Stone] typified by *Welwitsch 917* (Cogniaux 1891). Thus, when *O. welwitschii* was later transfered to *Dissotis*, Fernandes and Fernandes (1954) needed a nomen novum (*D. cogniauxiana*) since the name *D. welwitschii* was preoccupied based on a different type. Following the recent placement of *O. welwitschii* in *Heterotis* (Veranso-Libalah et al. 2017), the combination *H. cogniauxiana* (A.Fern. & R.Fern) Ver.-Lib. & G.Kadereit was made. However, under the Code (Turland *et al*. 2018), *H. cogniauxiana* is an illegitimate i.e. superfluous name (see Arts. 6.4 and 52.1), and the correct combination is *H. welwitschii* (see Art. 11.4, especially example 12).

Representative specimens examined.

ANGOLA. Mt. Tchivira. Lucondo Mission near NE corner of mountain, 1110 m elev., fl. 7 Oct. 2013, *Goyder et al*. 7373 (K!); Vila Arriaga, Mahita, fl. & fr. 25 Jan. 1962, *Correia 1798* (LISC barcode LISC030602! image); Cuanza Norte, Pungo Andongo, 1150 m elev., fl. 31 March 1937, *Exell & Mendonça 211*(LISC barcode LISC030603! image).

3. *Heterotis fruticosa* (Brenan) Ver.-Lib. & G.Kadereit, Taxon 66: 609. 2017.

Type: Nigeria, Ondo, about 3 km. E of Ondo, north of the Akure road, fl. 21 Sept. 1948 *Keay* 22569 (K barcode K000313157!; isolectotypes K K000313153!, FHI0022569! image!). Lectotype designated here.

(≡) *Dissotis rotundifolia var. fruticosa* Brenan, Kew Bulletin 5: 227. 1950.

(≡) *Dissotis fruticosa* (Brenan) Brenan & Keay, Kew Bulletin 7: 547. 1953.

Etymology

Named for the shrubby growth habit which distinguishes it from co-occurring species of *Heterotis*.

Phenology

Collected in flower and fruit in October.

Distribution and habitat

Idanre Hills, Ondo province in western Nigeria. "Shrubby vegetation among *Trilepis* (now *Afrotrilepis*) mats". 450–950 m elev.

Conservation status

This species is only confidently known from the Idanre Hills in Ondo province, western Nigeria. This small area of granite inselbergs only covers a few square kilometres, such that the extent of occurrence is inferred to fall within the threshold for the Critically Endangered category (< 100 km^2). It has only been collected from two of the inselberg 'hills', although it is likely that it occurs on additional, less accessible outcrops which have not been thoroughly surveyed. However, the total area of potentially suitable habitat at Idanre Hills is small; Richards (1957) observed that the *Trilepis* (now *Afrotrilepis*) mat community which *H. fruticosa* occurs in covered only about 20% of the surface of Carter's Peak, one of the two inselbergs which it has been recorded from. Thus, the area of occupancy is likely to be <10 km^2. There is inferred to be a continuing decline in the area, extent, and quality of habitat for this species due to wood cutting and clearance for cultivation of cash crops such as cocoa, pepper, corn, and bananas (Onadeko et al. 2014). Given the extremely restricted range and continuing decline of habitat, this species is preliminarily assessed as Critically Endangered B1ab(iii)+B2ab(iii).

Notes

In the protologue for this species' basionym, Brenan (1950) does not designate a holotype among the duplicates of *Keay* 22569, which are held at K and FHI. Keay (1953) cites 'typus speciei in Herb. Kew.', however, there are two sheets of *Keay* 22569 at K. We designate the K specimen with barcode K000313157 as the lectotype as it is the most representative, following Article 9.12 of the Code (Turland et al. 2018).

Representative specimens examined

NIGERIA. Ondo, Idanre Hills, Carter Peak, fl. 24 Oct. 1948, *Keay* 22583 (K barcode K002833085!); Ondo, A few yards to the U.H.F on a wet area on top of the mountain, fr. 4 Aug. 1974, *Daramola et al.* 71111 (K barcode K002833088!); Ondo, Idanre Hills; Carter Peak, fr. 29 Oct. 1949, Keay 25503 (K barcode K002833086!); Ondo, Idanre Hills, on east side of Orosun, fl. & fr. 30 Oct. 1949, Keay 25512 (K barcode K002833087!, FHI FHI0025512-0! image); Idanre hills, 30 km E of Ondo, about 3 km S of Idanre fl. & fr. 1 Oct. 1977 (K barcode K002833089!).

4. *Heterotis buettneriana* (Cogn.) Jacq.-Fél., Adansonia, n.s., 20: 418. 1981.

Bas.: *Osbeckia buettneriana* Cogn. ex Büttner, Verh. Bot. Vereins Prov. Brandenburg 31: 95. 1889.

Type: Lectotype (first-step lectotypification designated by Jacques-Félix (1971); second step-lectotypification designated here): Gabon, Ogôoué, *Thollon 444* (P barcode P00412569! image; isolectotypes: P00412568! image, P00412570! image). Additional syntype: Gabon, *Büttner 23* (B†).

Bas.: *Osbeckia buettneriana* Cogn. ex Büttner, Verh. Bot. Vereins Prov. Brandenburg 31: 95. 1889.

(≡) *Dissotis buettneriana* (Cogn.) Jacq.-Fél., Adansonia, n.s., 11: 547. 1971.

(=) *Osbeckia rubropilosa* De Wild., Pl. Bequaert. 1 : 378. 1922.

Type: Democratic Republic of the Congo, Avakubi, 30 Dec. 1913, *Bequaert 1678* (BR! BR0000005571147 image).

Etymology

Named for the German botanical collector Oskar Alexander Richard Büttner (1858-1927).

Phenology

Collected in flower and fruit between September–April.

Distribution and habitat

Cameroon, Equatorial Guinea, Gabon, Republic of Congo, Democratic Republic of Congo. Lowland evergreen forest and clearings. 50–800 m elev.

Conservation status

This species has a large extent of occurrence (EOO) of at least 900,000 km^2. It has been recorded from many more than ten locations and occurs in a range of different habitats, including disturbed sites. It is not thought that there any major threats impacting this species. It is preliminarily assessed as Least Concern.

Notes

In the absence of flowering material with which to examine the stamens, this species may be confused with *H. prostrata* due to its distinctly excurrent emergences at the apex of the sepals, which persist in fruit.

The protologue for this species' basionym (Cogniaux in Büttner 1889) lists two collections: *Buettner 23* and *Thollon 444*. The former was presumably destroyed at Berlin during World War II. The extant gathering *Thollon 444* (P) was subsequently designated by Jacques-Félix (1971) as a lectotype, however there are three sheets for *Thollon 444* in P. We designate the *Thollon 444* sheet with barcode P00412569 as the second-step lectotype because it is the only sheet with flowers in which the characteristic isomorphic stamens are clearly visible (Art. 9.17 of Turland et al. 2018).

Representative specimens examined

CAMEROON. Central Province, Mefou Proposed National Park Ndanan 2, 03.37°N 11.34° E, 700 m, fl. & fr. 22 March 2004, *Darbyshire* et al. *185* (K barcode K000023198!, YA, P); Central Province, Mefou Proposed National Park Ndanan 2, 03.37°N 11.34° E, 700 m, fl. 15 Oct. 2002, *Cheek* et al. *11111* (K barcode K000023197!, YA, WAG, SCA). **EQUATORIAL GUINEA.** Bata-Senge: Estrada km. 38 Bibogo, 650 m, fl. & fr. 9 April 1997, *Carvalho 6279* (NY! image, US! image, WAG! image, MA). **GABON**. Woleu-Ntem, chantier Oveng vers Mitzic, 0.40°N, 11.25 E, fl. & fr. 6 May 1986, *Louis 2163* (K barcode K002834366!, WAG); Ogooue-Maritime, former extraction road system accessible from Peni CBG chantier, 2°02.50' S, 10°24.98' E, fl. 28 Oct. 2005, *van Valkenburg* et al. *3013* (K barcode K002834367!, WAG). Estuaire, Libreville. P1: Arboretum de Sibang, 0° 25' N 9° 29' E, 50 m, fl. & fr. 7 Dec. 1999, *Simons* et al. *291* (WAG! image, MO! image, HNG, LBV). Goumina, (Mayombe), 100-200 m, fl. 1 dec. 1990, *la Croix 4986* (MO! image, BR! image). **DEMOCRATIC REPUBLIC OF CONGO**. Haut-Zaire. Ituri; Zone de Mambasa; ca. 14 km SSW of Epulu and 2 km S of Tito River on trail to Ituri River, summit of Mabobo Hill, 01° 16' 23"N 28° 32' 27"E, 790 m, fl. 2 Feb. 1994, *Gereau* et al. *5273* (BR! image, MO! image, WAG! image); Ituri; Zone de Mambasa; Basakwe Camp, west bank of Basakwe River ca. 4 km ESE of confluence of Edoro and Afarama Rivers, 01°32'24"N 028°32'41"E, 790 m, fl. 10 Feb. 1994, *Gereau & Bocian 5314* (MO! image); near Bafwasende, fl. & fr. 26 Sept. 1957, *Croockewit 700* (WAG! image).

5. *Heterotis decumbens* *(*P.Beauv.) Jacq.-Fél., Adansonia, n.s., 20: 418.

Bas.: *Melastoma decumbens* P.Beauv., Fl. Oware 1 : 69. 1806.

Type: « *Palisot de Beauvois s.n.* » (G G00014591! image) lectotype designated by Jacques-Félix (1983).

(≡) *Rhexia decumbens* (P.Beauv.) Poir. in Lam., Encycl., Suppl. 4 : 628. 1816.

(≡) *Osbeckia decumbens* (P.Beauv.) DC., Prodr. 3: 143. 1828.

(≡) *Asterostoma decumbens* (P.Beauv.) Blume, Mus. Bot. 1: 50. 1849.

(≡) *Dissotis decumbens* (P.Beauv.) Triana, Trans. Linn. Soc. London 28: 58. 1872 [1871].

(=) *Heterotis laevis* Benth., Niger Fl.: 348. 1849.

Type: Nun River, *Vogel 36* (K barcode K000313165!).

(≡) *Dissotis laevis* (Benth.) Hook.f., Fl. Trop. Afr. 2: 451. 1871.

(=) *Dissotis mahonii* Hook.f., Bot. Mag. 129: t. 7896. 1903.

Type: coll. Uganda 1901, cult. Kew 8 Sept. 1902, *Mahon 28* (K barcode K000313072!).

(=) *Dissotis decumbens* Triana *var. minor* Cogn. in A.L.P.P. de Candolle & A.C.P. de Candolle, Monogr. Phan. 7: 369. 1891.

Type: Democratic Republic of Congo, Bangala, fl. & fr. 8 June 1888, *Hens 164* (K barcode 000313104!, BR BR0000006493417! image, BR0000006494384! image).

Etymology

Named for its decumbent habit.

Phenology

Collected in flower and in fruit between October–June.

Distribution and habitat

Nigeria, Cameroon, Equatorial Guinea, Gabon, Republic of Congo, Democratic Republic of Congo, Central African Republic, South Sudan, Uganda, Tanzania, Angola. Introduced to Madagascar and the Mascarene Islands. Grows in forests and forest margins or clearings, along streams, roadsides, in plantations, and disturbed areas, sometimes creeping on boulders. 0–1,200 m elev.

Conservation status

This species is widespread with a very large range. It occurs at many more than ten locations and is suspected to have a large population size. It is not thought that there any major threats impacting this species. It is therefore preliminarily assessed as Least Concern.

Notes

Jacques-Felix (1983a; 1983b) effectively lectotypified *H. decumbens* (P.Beauv.) Jacq.-Fél by citing “Palisot de Beauvois, Nigeria (G!)” as the type. The stalked, stellate hypanthial emergences which otherwise characterise the genus *Heterotis* are reduced to setae or simple hairs in this species. In some specimens, the hypanthium is glabrescent. Whereas *H. prostrata* and *H. rotundifolia* appear to be widely naturalised across the tropics, this species is only known to be naturalised in Madagascar and the Mascarene Islands. All of the specimens of *Heterotis* from Madagascar and the Mascarene Islands examined in the preparation of this synopsis belonged to *H. decumbens*.

Representative specimens examined.

NIGERIA. Degema, Brass, fl. 14 December 1962, *Daramola & Aderson FHI 46329* (K barcode K002834257!). **CAMEROON.** Abong-Mbong, fl. 10 Sept. 1962, *Price & Evans 254* (K barcode K002834403!); South Region, south of Kribi, near new Kribi deep water port site, 2°42’18.0”N 9°51’49.1”E, fl. & fr. 16 October 2017, *van der Burgt et. al. 2151* (K barcode K001286879!, WAG, YA). **EQUATORIAL GUINEA.** Fernando Poo, fl. 27 Nov. 1946, *Guinea 258* (K barcode K002834410!). **GABON**. Estuaire, between Cap Santa Clara and Cap Esterias, 0°32.86’ N, 9°18.51’ E, 2 m elev., fr. 23 Feb. 2003, *Wieringa 4812* (K barcode K002834405!, WAG); Ogooue-Maritime, old logging road leading southward from chantier CBG Peni, 2°07.80’ S, 10°25.10’ E, 225 m elev., fl. 22 April 2005, *van Valkenburg* et al. *3156* (K barcode K002834406!, WAG); Nyanga, Bame, fishing camp, 60 km S of Mayomba, 27 km N of Congo Brazzaville border, 03°47’ 07” S, 11°01’ 01” E, fl. 11 May 2001, *Walters* et al. *640* (K barcode K002834407!, MO). **REPUBLIC OF CONGO**. Kouilou, Tchimpounga, Zone soleil 1, 4° 30’ 53.7” S, 11° 46’ 04.8” E, 5 m elev., fl. 5 Dec. 2012, *Mpandzou* et al. *1709* (K barcode K001393346!); Kouilov, Point 4, Noumbi, bloc Paris, 4° 5’ 58.0” S, 11° 20’ 11.0” E, 2 m elev., fl. & fr. 15 April 2013, *Nkondi* et al. *652* (K barcode K001393328!). **DEMOCRATIC REPUBLIC OF CONGO.** Boma, fr. 10 Oct. 1931, *Dacremont 68* (K barcode K002834408!, BR, WAG); Jardin D’Eala, fr. 22 May 1946, *Leonard 166* (K barcode K002834424!, BR). **CENTRAL AFRICAN REPUBLIC.** Ndakan, gorilla study area Njéké from M5400 to C 5800, 02°21’N 016°12’E, 350 m elev. fl. 7 May 1988, Harris & Fay 603 (MO! image). **SOUTH SUDAN.** Talanga, 4°01’ N, 32° 45’ E, 950 m elev., fr. 2 Dec. 1980, *Friis & Vollesen 638* (K barcode K002834472!), Khor Atiziri, fl. & fr. 28 Feb. 1870, *Schweinfurth 3093* (K barcode K002834473!). **UGANDA.** Entebe, 3900 ft elev., fl. 1901, *Fin. Michon s.n.* (K barcode K002834555!). **TANZANIA.** East shore, fr. Oct. 1893-1894, *Scott-Elliot 8232* (K barcode K002834558!) **ANGOLA.** fl. 1910 *Gossweiler* 4705 (K barcode K002834745!); near Loango River, fl. Oct. 1921, *Dawe 274* (K barcode K002834743!). **MASCARENE ISLANDS (INTRODUCED). REUNION.** Bord de zoute Le Tremblet, fl. 20 Nov. 1970, *Friedmann 629* (K barcode K002834785!)**;** **MADAGASCAR (INTRODUCED):** Antsiranana, Fivondronana d'Antalaha, Canton d'Ambohitralanana, à Andrahimbazaha, 15° 17' S, 50° 27' E, 0-60 m elev., fr. 29 April 1994, *Rahajasoa 367* (K barcode K002834784!)**;** Toamasina, Soanierana Ivongo, Antanambao-Andrangazaha, 16° 51'12" S, 49° 41'37" E, 0 m. elev., fr. 27 Nov. 2016, *Rakotoarisoa & Andriamahay SNGF 3840* (K barcode K000936861!, TAN, SNGF, TEF);

6. *Heterotis prostrata* (Thonn.) Benth. in Hooker Niger Fl.: 349. 1849.

Bas.: *Melastoma prostratum* Thonn. in Schumacher, Beskr. Pl.: 220. 1827.

Type: Ghana *Thonning 285* (C barcode C10004150! image) **lectotype here designated**; isolectotype C10004151! image).

(≡) *Dissotis prostrata* (Thonn.) Hook.f., Fl. Trop. Afr. 2: 452. 1871.

(≡) *Dissotis rotundifolia var. prostrata* (Thonn.) Jacq.-Fél., Adansonia, n.s., 11: 548 1971.

(=) *Dissotis deistelii* Gilg ex. Engl. in H.G.A. Engler & C.G.O. Drude, Veg. Erde 9(III 2): 748. 1921.

(=) *Dissotis schliebenii* Markgr., Notizbl. Bot. Gart. Berlin-Dahlem 12: 716. 1935.

Type: Tanzania, Muera Hochfläche, 60 km westlich Lindi, fl. 24 Feb 1935, *Schlieben 6068* (BM isotype! image).

(=) *Lepidanthemum triplinervium* Klotzsch in W.C.H. Peters, Naturw. Reise Mossambique 6(Bot. 1): 64. 1861.

(≡) *Heterotis triplinerva* (Klotzsch) Triana, Trans. Linn. Soc. London 28: 58. 1872 [1871].

(=) *Osbeckia zanzibariensis* Naudin, Ann. Sci. Nat., Bot., sér 3, 14: 55. 1850.

Type: *Bojer s.n.* (P P00412583! image).

Etymology

Named for its prostrate habit (i.e. lying flat on the ground).

Phenology

Collected in flower and fruit year-round.

Distribution and habitat

Ghana, Guinea, Sierra Leone, Côte d'Ivoire, Nigeria, Cameroon, Equatorial Guinea, Gabon, Republic of Congo, Democratic Republic of Congo, Uganda, Tanzania, Kenya, Angola, Zambia, Malawi, Zimbabwe, Mozambique. Grows in forests and forest margins or clearings, along streams, roadsides, in plantations, and disturbed areas, sometimes creeping on boulders.

Conservation status

This species is widespread with a very large range. It occurs at many more than ten locations and is inferred to have a large population size. It is not thought that there any major threats impacting this species. It is therefore preliminarily assessed as Least Concern.

Notes

There are two sheets of *Thonning 285* in C. We designate the sheet with barcode C10004150 as the lectotype, as it is most representative, following Article 9.12 of the Code (Turland et al. 2018).

Jacques-Félix (1971; 1983a) distinguished this species from *H. rotundifolia* based on elliptical rather than broadly ovate to suborbicular leaves, and sparser covering of emergences on the hypanthium, in addition to the character in the key presented in this synopsis: stellate emergences excurrent at the apex of the sepals (not excurrent in *H. rotundifolia*). All of these characters are variable within these two species, which have been synonymised in some past treatments (e.g. Jacques-Félix 1971). We deploy only the excurrent (*H. prostrata*) vs. non-excurrent (*H. rotundifolia*) sepal emergences in the key couplet for distinguishing these species as this appears to be the most consistent and recognisable difference between them. Yet some specimens of *H. prostrata* exhibit distinctly excurrent stellate emergences whereas in others, it is difficult to determine if the stellate cluster of hairs can be considered slightly excurrent or not. *Heterotis prostrata*, *H. decumbens*, and *H. rotundifo-*

lia may indeed comprise a species complex as suggested by Jacques-Félix (1981; 1995). Alternatively, intermediate forms could represent hybrids between *H. prostrata* and *H. rotundifolia*. Further work is necessary to clarify the species limits in this part of the genus.

Representative specimens examined

GUINEA: Kerouane, Langbalema Mt. ridge to N of Kerouane–Bamankoro road 09° 12’ 48’’ N, 9° 9’ 54’’ W, 745 m; fr. 29 Oct 2008; *Darbyshire 561* (K barcode K000615189!, HNG); **SIERRA LEONE:** fl. 2 April 1951, *Deighton 5389* (K barcode K002834267!); **COTE D’IVOIRE:** Abidjan; market of Adjamé; 3 June 1970, Koning 711 (WAG WAG.1096117! image); **NIGERIA**: Adamawa Division, Vogel Peak area, approx. 84° 25’ N, 11° 50’ E, 920 m elev., fl. 20 Nov 1957, *Hepper 1414* (K barcode K 002834318!); Benue Platue, Jos, Assob escarpment, 09° 30’ N, 08° 40’ E, fr. 22 April 1972, *Wit* et al. *1464B* (K barcode K002834320!); South E. State, Ikom, Abu village about 16 miles from Bende/Ayuk village on Abudu road, fl. 1 March 1973, *Latilo 67746* (K barcode K002834325!); **CAMEROON**: South West Province, Kupe-Muaneguba Division, Kupe Village Muanezum trail, 1200 m elev., fr. 28 March 1996, *Etuge 1840* (K barcode K000197738!, YA); South West Province, Mount Cameroon, Idenau, 2 m elev., fr. 17 Oct 1995, Dawson 35 (K barcode K000050228!, SCA, YA); Littoral Region, Ebo Proposed National Park, village, 04° 24’ 22.3’’ N, 10° 9’ 56.9’’ E, 100 m elev., fr. 3 Dec 2019, *Alvarez 34* (K barcode K001310318!); **EQUATORIAL GUINEA**: Bioco, Malabo-Brasilé, km 11, 220 m elev., fr. 25 July 1986, *Carvalho 2090* (K barcode K002834439!); **GABON**: About 20-40 km. NNE of Kouémayong, fr. 13 April 1988, *Breteler, Jongkind, & Dibata 8671* (K barcode K002834427!); **REPUBLIC OF CONGO**: Léopoldville, Thysville, fr. 28 Jan 1950, *Compére 1371* (K barcode K002834458!); **DEMOCRATIC REPUBLIC OF CONGO**: Riviere Kalamu, Makala (ville de Kinshasa), fl. 18 Nov 1976, *Breyne 3486* (WAG barcode WAG.1092457! image); **UGANDA**: Rabongo Forest, approx. 2° 6’ N, 52° E, 1020 m elev., fl. & fr. 12 May 1993, Sheil 1636 (K barcode K002834560!); **TANZANIA**: Magewga Estate. dist. Korogwe, fl. 15 April 1952, *Faulkner 984* (K barcode K002834614!); Magila nr Muhesh, 600 m elev., fl. 8 Nov 1970, *Archbold 1290* (K barcode K002834611!); Amani, fr. 21 Dec 1949, *Verdcourt 8* (K barcode K002834610!); **KENYA:** K7, Kwale District, Gongoni For Res NE side, 30 m elev., fl. 2 June 1990, *Robertson & Luke 6346* (K barcode K002834559!); K7 Kwale District, Shimba Hills, fr. 1 April 1968 *Magogo & Glover 609* (K barcode K002834582); K7 Kilifi District, just north of Mariakani, fl. & fr. 8 March 1977, *Hooper & Townsend 1256* (K barcode K002834580!); **ANGOLA**: Malange, s.d., *Gossweiler 1275* (K barcode K002834782!); **ZAMBIA**: Mwinilunga District. Road to Congo border., 1290 m elev., fl. 14 Nov 1962, *Richards 17208* (K barcode K002834764!); Rapids Mwinilunga, fr. 20 May 1969, *Mutimushi 3229* (K barcode K002834766!); **MALAWI**: Northern Region, Nkhata Bay District. 5 km W of Nkhata Bay, by road in Kandoli Forest Reserve, 550 m elev., fl. 6 March 1982, *Brummitt* et al. *16343* (K barcode K002834761!); fl. & fr. 2 Feb 1955, *Jackson 1440* (K barcode K002834758!); **ZIMBABWE**: District Melsetter; Haroni River, 457 m elev., fl. 24 April 1962, *Wild 5733* (K barcode K002834769!); **MOZAMBIQUE**: Moramballa, fr. 30 Dec 1858, *Kirk s.n.* (K barcode K002834752!); Niassa, Cabo Delgado, Palma, andados 14 km de Palma para Nangade, 50 m elev., fl. 18 April 164, *Torre & Paiva 12132* (K barcode K002834747!); Manica, Chimanimani foothills, Maronga, Chiira River, west of Comeni’s compound, 19° 58’ 33’’ S, 33° 05’ 14’’ E, 342 m elev., fl. 14 Nov 2015, *Darbyshire 906* (K barcode K001187553!).

7. *Heterotis rotundifolia* (Sm.) Jacq.-Fél., Adansonia, n.s., 20: 417.1981.

Bas.: *Osbeckia rotundifolia* Sm., Cycl. [A. Rees], London. 1819.

Type: Sierra Leone *Afzelius s.n.* (BM BM000902398! image) lectotype designate by Jacques-Félix (1983); isolectotype LINN LINN-HS653-4! image).

(≡) *Asterostoma rotundifolia* (Sm.) Blume, Mus. Bot. 1: 50. 1849.

(≡) *Dissotis rotundifolia* (Sm.) Triana, Trans. Linn. Soc. London 28: 58. 1872 [1871].

(=) *Kadalia rotundifolia* Raf., Sylva Tellur.: 101. 1838.

(=) *Melastoma plumosum* D.Don, Mem. Wern. Nat. Hist. Soc. iv.: 290. 1823.

(≡) *Heterotis plumosa* (D.Don) Benth., Niger Fl.: 348. 1849.

(≡) *Dissotis plumosa* (D.Don) Hook.f., Fl. Trop. Afr. 2: 452. 1871.

Etymology

Named for its round, orbicular leaves.

Phenology

Collected in flower and fruit year-round.

Distribution and habitat

Guinea, Sierra Leone, Liberia, Nigeria, Cameroon, Equatorial Guinea, Gabon, Republic of Congo. Grows in forests and forest margins or clearings, along streams, roadsides, in plantations, and disturbed areas, sometimes creeping on boulders.

Conservation status

This species is widespread with no known major threats. It has been assessed as Least Concern on the IUCN Red List (Ghogue 2020).

Notes

Jacques-Felix (1983a) effectively lectotypified *H. rotundifolia* (Sm.) Jacq.-Fél. by citing "Afzelius (BM), Sierra Leone" as the type.

In the preparation of this synopsis, many specimens determined as *H. rotundifolia* were found to have distinctly excurrent emergences at the apex of the sepals, placing them in *H. prostrata*. In particular, all of the specimens examined from East Africa were either redetermined as *H. prostrata* or exhibited somewhat intermediate morphology. *H. rotundifolia* is likely less widespread in tropical Africa than presumed, and is possibly restricted to West tropical Africa, as suggested by Jacques-Félix (1971; 1983a). Further work is necessary to determine the species limits in this genus and in this treatment we exclude intermediate specimens.

Representative specimens examined

GUINEA. Guinée Maritime, Boké Préfecture, Kabata, Route de Kabat avers l'ouest, 10° 42' 59" N, 14° 34' 16" W, 10 m elev., fr. 24 Nov 2007, *Camara 85* (K barcode K000460542!, HNG); Simandou Range, Moribadou to Canga East, 08° 35' 36" N, 07° 51' 28" E, 800 m elev., fl. 8 July 2006, *Cheek 13312* (K barcode K000436912!); Préfecture de Coyah, Kakoulima, 09° 46' 51.7" N, 13° 26' 02.8" W, 542 m elev., fl. 1 Dec 2018, *Konomou* 632 (K barcode K001310314!); **SIERRA LEONE**. Gola National Park, central block, 07° 39' 38.2" N, 10° 51' 34.8" W, 370 m elev., fl. 03 Oct 2013, *Sesay 105* (K barcode K001243830!); Northern Region, Tonkolili District, Sula Mts., Bantho Hill ridge above Bongbonga village, WNW of Numbara Hill, 09° 03' 05" N, 11° 40' 30" W, 750 m elev., fr. 02 Dec 2009, *Darbyshire 609* (K barcode K000191460!, SL, FBC); Fourah Bay College, fl. 3 Oct 1967, *Morton & Jarr SL4953* (K barcode K002834268!); **LIBERIA**. Zorzor–Gbarnga road, west of St. Paul river, fl. 27 July 1966, *Bos 2168* (K barcode K00283577!); Nimba, 450 m elev., 6 Oct 1971, *Adam 26228* (K barcode K002834278!); 3 miles northeast of Suacoco, Gbarnga, Central Province, fl. 11 Oct 1950, *Daniel 24* (K barcode K002834284!); **NIGERIA**. West, Ekiti, On the new road from Imesi-Igbajo, fl. 23 Oct 1972, *Latilo & Fagemi 67514* (K barcode K002834323!); near Port Harcourt, on cleared ground 7 miles to N.E., fl. 24 Sept 1942, *Taylor 7* (K barcode K002834327!); West state, Ibadan district, bush near Forestry School, fl. 20 Oct 1971, *Wit 734* (K barcode K002834322!); **CAMEROON**. Cameroons Mnt, Above Buea, 1050 m elev., fl. 30 March 1952, *Morton 6733* (K barcode K000050229!); **EQUATORIAL GUINEA**. Canetera de Musola, Fernando Poo, fr. 11 Jan 1947, *Guinea 1259* (K barcode K002834440!); **GABON**. Ogooué-Maritime, Rabi-Kounga, c. 01° 42' S, 09° 52' E, fr, 16 Nov 1991, *Schoenmaker 152* (K barcode K002834444!); Mitzic, 00° 47' N, 11° 34' E, 800 m elev., fl. 28 Aug 1957, *Holderness 282* (K barcode K002834446!); **REPUBLIC OF CONGO**. Lekoumou Préfecture, Yakatopema (Moukouma), New MPD Camp. Forest patch at side of old village, Mousaou-junction with road, 500m from new village, 02° 53' 21.0" S, 13° 36' 44.0" W, fl. 29 Jan 2009, *Kami 4198* (K barcode K000518748!); fl. 1860, *Grey s.n.* (K barcode K002834454!)

DISCUSSION

The genus *Heterotis* is widely naturalised across much of the tropics. Most specimens and records from outside of Africa are determined as *H. rotundifolia*, commonly called "Pink Lady", which is classified as a weed or alien invasive species in several regions, including Puerto Rico, Australia, Singapore, and several Pacific islands (CABI 2014). However, there are also records of *H. prostrata* and *H. decumbens* from outside of mainland Africa, and the distribution of each species outside of their native ranges has not been clarified. In this synopsis, we only list the naturalised occurrences of *H. decumbens* which could be verified with specimens held at K: all of the collections of this genus at K from Madagascar and the Mascarene Islands are *H. decumbens*. Citing Bakhuizen van den Brink (1943) and Almeda (1990), Jacques-Félix (1995) suggested that early introductions to Java and Hawaii respectively both represent *H. rotundifolia*. However, Veranso-Libalah et al. (2017) state that the widely naturalised *Heterotis* across Asia, North America, Oceania, Central America and the Caribbean is in fact *H. prostrata*, wrongly identified as *H. rotundifolia*. It is difficult to distinguish between these species from photos due to the necessity of careful examination of the apices of the sepals. However, citizen science records on iNaturalist suggest that both of these species are naturalised and potentially invasive outside of their native range (iNaturalist 2025), with many observations appearing to represent intermediate specimens.

Whereas at least three species of *Heterotis* are widespread and even naturalised and invasive outside of their native range, the genus contains two species preliminarily assessed in threatened categories according to IUCN Red List criteria, including the newly described, narrowly endemic *H. kupensis*. Cheek and Onana (2021) list 25 endemic and 30 near-endemic plant species currently known from Mt Kupe, of which 18 were not yet formally described at the time. The description of these new species is an urgent task; most undescribed species are threatened (Brown *et al.* 2023), yet their conservation status cannot be assessed for the IUCN Red List of Threatened Species until they are formally named. The description and assessment of threatened species is also critical for insuring their conservation *in situ*, for example through the identification and designation of Tropical Important Plant Areas (TIPAs) (Darbyshire et al. 2017). We herein contribute to the effort to characterise the endemic and unknown flora of Mt Kupe by formally describing *H. kupensis*, a species which was first recognised as new to science twenty years prior but has remained unnamed until now (Cheek et al. 2004). We provisionally assess *H. kupensis* as Vulnerable, providing further support for the protection of Mt Kupe as a critical site for preserving threatened and endemic plant diversity. Mt Kupe is designated as one of Cameroon's most high ranking Important Plant Areas with 145 threatened species on the IUCN Red List as of 2022, of which 19 are Critically Endangered, within its 145 km^2 (Murphy et al. 2023). It currently has no formal protection.

The new species described here is best placed in the genus *Heterotis* on the basis of morphological evidence. However, we caution that there is currently no mature fruiting material, precluding the description of seed characters which are an important trait for generic delimitation in Melastomateae, including for *Heterotis*. Further, the staminal morphology is entirely unique for the genus. *Heterotis kupensis* also diverges from other members of the genus as characterised by Veranso-Libalah *et al.* (2017) in that it is an erect herb with stems that are woody at the base, rather than a decumbent herb. However, we note that both *Heterotis fruticosa* and *H. welwitschii* are also upright subshrubs, and some specimens of typically decumbent or prostrate species in the genus appear to be somewhat fruticose. We therefore suggest that habit is not a reliable diagnostic feature for the genus.

We attempted to generate DNA sequences for the markers used by Veranso-Libalah et al. (2017) in order to provide molecular support for this species' placement in *Heterotis* but were unable to extract good DNA from the type specimen. Future collections of this species may reveal intraspecific variation, seed traits, or molecular evidence which may prompt re-examination of its generic placement within Melastomateae. However, we consider its description an urgent task given its narrow endemicity and apparent vulnerability to extinction, and we therefore describe it here as a morphologically unique member of *Heterotis*.

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REFERENCES

Almeda F. 1990. Manual of the Flowering Plants of Hawaii. Chapter 65, Melastomataceae: 903–917.

Bakhuizen van den Brink RC Jr. 1943. A contribution to the knowledge of the Melastomataceae occurring in the Malay Archipelago especially in the Netherlands East Indies. Mededeelingen van het Botanisch

Museum en Herbarium van Rijks Univesrsiteit te Utrecht. 91:1–391.

Bentham G. 1849. Melastomaceae. In: Hooker WJ. (Ed.), Niger Flora. London: Hippolyte Baillière; p. 344–358. https://doi.org/10.5962/bhl.title.594

Brenan JPM. 1950. More new plants from the Idanre Hills, Nigeria. Kew Bulletin. 5(2):227–232. https://doi.org/10.2307/4117229

Brown M, Bachman S, Lughadha EN. 2023. Three in four undescribed plant species are threatened with extinction. New Phytologist. 240:1340–1344. https://doi.org/10.1111/nph.19214

Büttner R. 1889. Neue Arten von Guinea, dem Kongo und dem Quango. Verhandlungen Botanischen Vereins Provinz Brandenburg. 31:64–96.

CABI (Centre for Agriculture and Bioscience International). 2014. *Heterotis rotundifolia* (pink lady). In: Invasive Species Compendium. [accessed 2025 Aug 15]. http://www.cabi.org/isc/datasheet/120226

Cable S, Cheek M. 1998. The Plants of Mt Cameroon: a conservation checklist. Royal Botanic Gardens, Kew.

Chapman J, Chapman H. 2001. The forests of Taraba and Adamawa States, Nigeria: an ecological account and plant species checklist. Christchurch,University of Canterbury.

Cheek M, Alvarez-Aguirre MG, Grall A, Sonké B, Howes M-JR, Larridon I. 2018. *Kupeantha* (Coffeeae, Rubiaceae), a new genus from Cameroon and Equatorial Guinea. PLoS One. 13(6):e0199324. https://doi.org/10.1371/journal.pone.0199324

Cheek M, Cable S, Hepper FN, Ndam N, Watts J. 1996. Mapping plant biodiversity on Mount Cameroon. In: van der Maesen LJG, van der Burgt XM, van Medenbach de Rooy JM, editors. Biodiversity of African Plants. Proceedings of the XIVth AETFAT Congress; Aug 22–27; Wageningen, Netherlands. Dordrecht: Kluwer. Pp. 110–120. https://doi.org/10.1007/978-94-009-0285-5_16

Cheek M, Etuge M, Williams S. 2019. *Afrothismia kupensis* sp. nov. (Thismiaceae), Critically Endangered, with observations on its pollination and notes on the endemics of Mt Kupe, Cameroon. Blumea. 64(1):158–164. https://doi.org/10.3767/blumea.2019.64.02.06

Cheek M, Onana J, Pollard BJ. 2000. The plants of Mount Oku and the Ijim Ridge, Cameroon: a conservation checklist. Royal Botanic Gardens, Kew.

Cheek M, Pollard BJ, Darbyshire I, Onana JM, Wild C. 2004. The plants of Kupe, Mwanenguba and the Bakossi Mts, Cameroon: a conservation checklist. Royal Botanic Gardens, Kew.

Cheek M, Achoundong G, Onana JM, Pollard B, Gosline G, Moat J, Harvey YB. 2006. Conservation of the plant diversity of Western Cameroon. In: Proceedings of the 17th AETFAT Congress; Addis Ababa, Ethiopia. p. 779–791.

Cheek M, Harvey YB, Onana JM. 2010. The plants of Dom, Bamenda Highlands, Cameroon: a conservation checklist. Royal Botanic Gardens, Kew.

Cheek M, Harvey Y, Onana J. 2011. The plants of Mefou Proposed National Park, Yaoundé, Cameroon: a conservation checklist. Royal Botanic Gardens, Kew.

Cheek M, Onana JM. 2021. The endemic plant species of Mt Kupe, Cameroon with a new Critically Endangered cloud-forest tree species, *Vepris zapfackii* (Rutaceae). Kew Bulletin. 76(4): 721–734. https://link.springer.com/article/10.1007/s12225-021-09984-x

Cheek M, Soto Gomez M, Graham SW, Rudall PJ. 2024. Afrothismiaceae (Dioscoreales), a new fully mycoheterotrophic family endemic to tropical Africa. Kew Bulletin. 79(1): 55–73. https://link.springer.com/article/10.1007/s12225-023-10124-w

Chen L, van der Burgt X, Haba P, Kadereit G, Veranso-Libalah MC. 2025. Phylogenomics of African Melastomateae (Melastomataceae): Revisiting generic relationships, placement of three enigmatic taxa and description of two new genera. Taxon. 74: 857–873. https://doi.org/10.1002/tax.13349

Cogniaux CA. 1891. Melastomaceae. In: de Candolle A, de Candolle C, editors. Monographiae Phanerogamarum. [A.DC. & C.DC.] 7. Paris: Sumptibus G. Masson. https://doi.org/10.5962/bhl.title.45961

Darbyshire I, Anderson S, Asatryan A, Byfield A, Cheek M, Clubbe C, Ghrabi Z, Harris T, Heatubun CD, Kalema J, Magassouba S. 2017. Important Plant Areas: revised selection criteria for a global approach to plant conservation. Biodiversity Conservation. 26(8): 767–1800. https://link.springer.com/article/10.1007/s10531-017-1336-6

Fernandes A, Fernandes R. 1954. Sur la position systématique de la section *Pseudodissotis* Cogn. du genre *Osbeckia* L. (Note préliminaire). Boletim Sociedade Broteriana sér 2. 28: 65–76.

Fernandes A, Fernandes R. 1969. Melastomataceae africanae novae vel minus cognitae V. Boletim Sociedade Broteriana. sér 2. 43: 285–306.

Figueiredo E, Smith GF. 2008. Plants of Angola / Plantas de Angola. Pretoria, SANBI.

GBIF. 2024. Global Biodiversity Information Facility. [accessed 2024 Aug 23]. https://www.gbif.org/

Farr ER, Zijlstra G. (Eds.). 1996+. Index Nominum Genericorum (Plantarum). [accessed 2025 Aug 28]. http://botany.si.edu/ing/

Gilbert MG. 1995. Melastomataceae. In: Edwards S, Mesfin T, Hedberg I. (Eds.), Flora of Ethiopia and Eri-

trea. 2(2): 265–380. Addis Ababa and Uppsala: The National Herbarium and The Department of Systematic Botany, Uppsala University.
Ghogue P. 2020. *Heterotis rotundifolia*. The IUCN Red List of Threatened Species 2020:e. T136663037A136663043. Accessed 09 Nov 2024. https://doi.org/10.2305/IUCN.UK.2020-2.RLTS.T136663037A136663043.en
Harvey YB, Pollard BJ, Darbyshire I, Onana JM, Cheek M. 2004. The plants of Bali Ngemba Forest Reserve, Cameroon: a conservation checklist. Royal Botanic Gardens, Kew.
Harvey Y, Tchiengué B, Cheek M. 2010. The plants of the Lebialem Highlands: a conservation checklist. Royal Botanic Gardens, Kew.
iNaturalist contributors, iNaturalist (2025). iNaturalist Research-grade Observations. iNaturalist.org. Occurrence dataset https://doi.org/10.15468/ab3s5x accessed via GBIF.org on 2025-08-29.
IUCN. 2012. IUCN Red List Categories and Criteria, Version 3.1. 2nd ed. Gland (Switzerland) and Cambridge (UK): Species Survival Commission, International Union for Conservation of Nature; [accessed 2025 Aug]. Available from: http://www.iucnredlist.org/
IUCN Standards and Petitions Committee. 2024. Guidelines for using the IUCN Red List Categories and Criteria, Version 16. Gland (Switzerland): International Union for Conservation of Nature; [accessed 2025 Aug]. Prepared by the Standards and Petitions Committee. Available from: https://www.iucnredlist.org/documents/RedListGuidelines.pdf
Jacques-Félix H. 1971. Note sur trois mélastomatacées d'Afrique. Adansonia, sér 2. 11(3): 546–549.
Jacques-Félix H. 1981. Observations sur les caractères staminaux et la classification des Osbeckieae (Melastomataceae) capsulaires africaines. Adansonia, sér 2. 20(4): 405–429.
Jacques-Félix H. 1983. Fl. Cameroun 24, Mélastomatacées. Yaoundé,Délégation Générale à la Recherche Scientifique et Technique.
Jacques-Félix H. 1995. Histoire des Melastomataceae d'Afrique. Bull Mus Natl Hist Nat, B, Adansonia. 16(2-4): 235–311.
Keay RWJ. 1953. Revision of the "Flora of the West Tropical Africa": II. Kew Bulletin. 7(4): 543–548. https://doi.org/10.2307/4117809
Maisels FG, Cheek M, Wild C. 2000. Rare plants on Mount Oku summit, Cameroon. Oryx. 34(2): 136–140. https://doi.org/10.1046/j.1365-3008.2000.00107.x
Murphy B, Onana JM, van der Burgt XM, Ngansop Tchatchouang E, Williams J, Tchiengué B, Cheek M. 2023. Important Plant Areas of Cameroon. Royal Botanic Gardens, Kew.
Onadeko AB, Rödel MO, Liedtke HC, Barej MF. 2014. The rediscovery of Perret's toad, *Amietophrynus perreti* (Schiøtz, 1963) after more than 40 years, with comments on the species' phylogenetic placement and conservation status. Zoosystematics and Evolution. 90(2): 113–119.
Richards PW. 1957. Ecological notes on West African vegetation: I. The plant communities of the Idanre hills, Nigeria. Journal of Ecology. 45: 563–577. https://doi.org/10.2307/2256936
Stone RD, Ghogue JP, Cheek M. 2008. Revised treatment of *Memecylon* sect. *Afzeliana* (Melastomataceae: Olisbeoideae), including three new species from Cameroon. Kew Bulletin. 63(2): 227–241. https://link.springer.com/article/10.1007/s12225-008-9033-y
Thiers B. continuously updated. Index Herbariorum: a global directory of public herbaria and associated staff. New York (NY): New York Botanical Garden's Virtual Herbarium; [accessed 2025 Apr]. http://sweetgum.nybg.org/ih/
Triana J. 1872. Les Mélastomacées. Transactions of the Linnaean Society London. 28(1): 1–188.
Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber WH, Li DZ, Marhold K, et al. 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile. 159. Glashütten (DE): Koeltz Botanical Books.
Veranso-Libalah MC, Stone RD, Fongod AG, Couvreur TL, Kadereit G. 2017. Phylogeny and systematics of African Melastomateae (Melastomataceae). Taxon. 66(3): 584–614. https://doi.org/10.12705/663.5
Veranso-Libalah MC, Stone RD, Kadereit G. 2020. Towards a complete phylogeny of African Melastomateae: Systematics of *Dissotis* and allies (Melastomataceae). Taxon. 69(5): 946–991. https://doi.org/10.1002/tax.12317
Veranso-Libalah MC, Stone RD, Kadereit G, Guimarães PJF. 2022. Systematics and Taxonomy of the Tribe Melastomateae. In: Goldenberg R, Michelangeli FA, Almeda F, editors. Systematics, Evolution, and Ecology of Melastomataceae. Springer. https://doi.org/10.1007/978-3-030-99742-7_21
Wickens GE. 1975. Melastomataceae. In: Polhill RM, editor. Flora of Tropical East Africa. London: Crown Agents for Oversea Governments and Administrations.

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A synoptic revision of the creeping herbaceous African species of *Ardisia* (Primulaceae or Myrsinaceae) with six new species from Cameroon and Gabon

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Abstract. Currently 39 species of *Ardisia* are recognised from continental Africa, of which three (*A. sadebeckiana* Gilg, *A. schlechteri* Gilg, and *A. ebo* Cheek, each endemic to Cameroon and known from a single collection) are herbaceous, with creeping, horizontal, rooting herbaceous stems, the stem apex more or less ascending to up to c. 10 cm tall above the ground (decumbent). These species lack the distinctive plagiotropic (perpendicular and horizontal) aerial reproductive stems seen in most woody *Ardisia* species of Africa (instead sporadically producing rooting ascending stems from the horizontal stem) and have distichous leaves (not spiralled as in most species in Africa). Accordingly, they are proposed as a separate subgenus *Kamardisia*. Study of herbarium material revealed that six additional species exist which are described and illustrated in this paper, together with preliminary conservation assessments. These are: *A. hansii* (South Region, Cameroon and Belinga, Gabon), *A. massaha* (Belinga, Gabon), *A. chaillu, A. minuta, A. waka* (all Chaillu Massif, Gabon), *A. ngounie* (Ogooué-Maritime, Gabon). We provide a key to the identification of the nine herbaceous species, provide preliminary conservation assessments for each, and notes on shared characteristics of the African herbaceous species including the taxonomic value of leaf microcharacters (oil glands and trichomes). We also make a preliminary report on the possibility of bacterial colonisation of marginal leaf pores in some of these herbaceous species. All of the species are range restricted, the most wide-ranging with only three sites. All but one species is threatened, and almost all of those are Critically Endangered (provisional assessments). The two first published species have not been seen for more than 125 years, despite being in easily accessible, well-botanised locations, and are both feared extinct. We discuss actions to attempt to refind these species and safeguard the remainder.

Keywords: ardisiaquinones, bacterial nodules, conservation, extinct species, *Paraburkholderia.*

INTRODUCTION

Ardisia Sw. (Swartz 1788) is a genus placed in the family Primulaceae or Myrsinaceae (Julius et al. 2021; Ståhl and Anderberg 2004). The genus is pantropical, estimates of the total number of species vary from 400 to c. 1000 species (POWO continuously updated; Julius et al. 2021; Ståhl and Anderberg 2004). New species to science are continually being published, especially from Asia e.g. China (Mao, Hu 2013 and Quan, Tan 2024), Vietnam (Nuraliev et al. 2021), the Philippines (Magtoto et al. 2021), and above all from Malaysia (Julius and Utteridge 2012, 2021, 2022; Julius et al. 2017, 2023).

In Africa, the species are mainly shrubs of evergreen forest understorey. A small number of Asian species are cultivated e.g. *Ardisia crenata* Sims (also known as coralberry or Christmas berry), in gardens due to its attractive red berries that persist through winter and its glossy, evergreen foliage. *Ardisia crispa* (Thunb.) A.DC is similarly planted https://www.rhs.org.uk/plants/30319/ardisia-crispa/details.

Ardisia japonica Blume is cultivated as a groundcover plant. The genus is known in Asia for being of value in traditional medicine. Species have been used for the treatment of cancer, hypertension, irregular menstruation, gonorrhea, diarrhea and postnatal syndromes, among others. The chemical basis of these uses was reviewed by Liu et al. (2022). Among the compounds produced are alkylbenzoquinones, specifically ardisiaquinones. In one African species these compounds have been shown to have antiproliferative and antimicrobial properties (Dzoyem et al. 2014).

In Africa, many species of *Ardisia* are range-restricted, and as a result threatened with extinction. Of the c. 40 species accepted, 12 have been assessed for their extinction risk level on the IUCN Red List, all but two of which are Cameroonian. The assessments were mainly on the basis of Cable and Cheek (1998) and Onana and Cheek (2011). Of the ten Cameroonian species assessed seven are Critically Endangered, the highest level of threat (e.g. *Ardisia etindensis* Taton, in Cheek and Cable 2000a).

Many of the species now included in the genus *Ardisia* have been included in other genera, some of which have in recent decades been synonymised with *Ardisia* e.g. *Tetrardisia* Mez (Larsen & Hu 1995). Large scale molecular phylogenetic studies show that several accepted genera are embedded in the wider genus *Ardisia*, especially in Asia (Julius et al. 2021 using nrITS; Larson et al. 2023 using 353 nuclear markers).

Most continental African *Ardisia* species were formerly included in the genus *Afrardisia* Mez (Mez 1902). The continental African species of *Ardisia* (based on a sample of four taxa) form a single subclade in Julius et al. (2021) suggesting they are monophyletic. In contrast, in Larson et al. (2023) the two continental African taxa included in the study appear embedded in separate subclades of mainly Asian species including one as sister to the accepted segregate genus *Fittingia* Mez (Mez 1902).

Baker (in Oliver 1877) published the first two tropical African species, from Sao Tomé and Gabon. Twenty-five years later, eight further species from Cameroon were published (Gilg 1902). In the same year, Mez (1902) grouped all ten then known African species into his newly erected genus *Afrardisia,* separated from *Ardisia* by a single character: the ovules were stated to be uniseriate (not biseriate or multiseriate as in *Ardisia sensu stricto*). In 1913, nine further new species, one from the Democratic Republic of the Congo (DRC, formerly Belgian Congo) and eight from Cameroon, were published by Gilg and Schellenberg (1913). De Wildeman (1925), Good (1927) and Perrier de la Bâthie (1953) then published three new species, respectively from DRC, Angola (Cabinda) and from Madagascar. De Wit (1958) revised the genus *Afrardisia*. He described a new species from Brazzaville, Republic of Congo, and synonymised six other species (*A. brunneo-purpurea* Gilg, *A. haemantha* Gilg, *Afrardisia ledermannii* Gilg & Schellenb., *Afrardisia hylophila* Gilg & Schellenb., *Afrardisia dentata* Gilg & Schellenb. and *Afrardisia rosacea* Gilg & Schellenb.). De Wit excluded the only species described from Madagascar at that point (*Afrardisia didymopora* H.Perr.) from the genus. He also neotypified many names for which types had been destroyed at B in 1943. Capuron (1963) described a further new species from Madagascar.

Taton (1979) showed that the placentation character used by Mez to separate the African species from the rest of the genus, breaks down, making *Afrardisia* a synonym of *Ardisia*. Accordingly, he transferred names from *Afrardisia* making six new combinations in *Ardisia*. He also published eighteen new species, one from DRC, ten from Cameroon, one from the Republic of Congo and six from Gabon. Taton and Lejoly (1980) published *A. lisowskii* Taton & Lejoly from DRC. In 2010, Cheek published two new species from Cameroon (Cheek in Cheek et al. 2010). *Ardisia ebo* Cheek (Cheek and Xanthos 2012) was published from Cameroon and Gabon. Up to this point, a total of thirty-nine species of continental African *Ardisia* have been published and accepted (African Plant Database, continuously updated).

African *Ardisia* have been treated in several regional and national Flora and checklist accounts. Sixteen species in the genus *Ardisia* from Gabon have been recognized (Sosef et al. 2006). In Cameroon, twenty-two species in the genus *Ardisia* have been accepted (Onana 2011), the highest number for any tropical African country. In the Flora of West Tropical Africa, a total of seven species (published under the formerly recognized genus *Afrardisia*) are recognized, all from eastern Nigeria and adjoining former British Cameroon (Hepper 1963). For the Flora of tropical East Africa, only two species in the genus *Ardisia* are recognised, one of which, in Zanzibar, remains unnamed and dubious (Halliday 1984). In DRC, a total of ten species in the genus *Ardisia* have been accepted (Taton 1980). The genus has not been recorded in the Flora Zambesiaca, nor the Flora of southern Africa areas.

The African species are all understorey species of evergreen forest from sea-level to 2400 m alt. The majority are shrubs or small trees of 0.3–2(–20) m tall. These woody species generally have an erect principal (orthotropic) vegetative axis from which horizontal plagiotropic reproductive branches arise in most species. The plagiotropic shoots are widened and laterally flattened at their base as occurs also in many of the Asian species.

African herbaceous creeping Ardisia

Among the known species of African *Ardisia*, three are unusual in being herbaceous and decumbent to procumbent, with long horizontally creeping and rooting, slender, flexible stems that do not increase in thickness with age/distance from stem apex. The stems terminate with a short (< 10 cm tall), more or less ascending, leafy reproductive part, which if decumbent produces long aerial adventitious roots which appear contractile, pulling the lower aerial part of the stem towards the ground. The elongating stem apex thus remains more or less fixed in height above the ground. New shoots arise at intervals from the horizontal surface/subterranean stem about 15–20 cm distant from the apex of the principal axis. The new shoots root, propagating vegetatively and by repetition form carpets on the floor of the forest (e.g. *A. ebo,* Cheek and Xanthos 2012). In these herbaceous creeping species plagiotropic branches are not produced (Cheek and Xanthos 2012). The known African herbaceous species are *A. schlechteri* Gilg, *A. sadebeckiana* Gilg and *A. ebo* Cheek, all of low altitude evergreen rainforest in coastal Cameroon. The first two species were collected in the 1890s, published (Gilg 1902) and have not been found since, leading to concerns that they are extinct.

In preparation for revising *Ardisia* for the accounts for the Flore du Gabon and the Flore du Cameroun as steps towards revising all the continental African species, it was decided to begin with the herbaceous taxa. In the paper describing *Ardisia ebo*, significant heterogeneity in leaf micro-structures was recorded among the specimens, warranting further taxonomic investigation (Cheek & Xanthos 2012). Material of herbaceous taxa collected from Gabon and Cameroon subsequent to Taton's synoptic revision (Taton 1979) was also studied, resulting in the discovery of the several taxonomic novelties recorded in this paper.

MATERIAL AND METHODS

This study is mainly based on the herbarium specimens, including corresponding field notes, at the herbaria of the Royal Botanic Gardens, Kew (K), Natural History Museum U.K. (BM), National Museum of Natural History, Paris, France (P) and National Herbarium of Cameroon (YA). Herbarium loans included those from the Wageningen herbarium at Naturalis, Leiden, the Netherlands (WAG) and Meise Botanic Garden, Belgium (BR). It was not possible to obtain specimens from BRLU due to digitising operations, nor was it possible to access specimens at LBV and YA. The study is also based on the study of digital images of herbarium specimens from other herbaria e.g. Herbarium Hamburgense (HBG) via GBIF (continuously updated). However, digital images do not give the resolution needed for comprehensive taxonomic studies since insufficient or no detail of trichomes and internal leaf structures can be observed, which are often diagnostic at species level. Herbarium codes follow Index Herbariorum (Thiers continuously updated). All specimens cited have been seen unless indicated "n.v.". Herbarium practices and procedures follow Davies et al. (2023). Nomenclatural changes were made according to the International Code of Nomenclature for algae, fungi, and plants (Turland et al. 2018). Names of species and authors follow IPNI (continuously updated). Herbarium material was examined with a Leica Wild M8 dissecting binocular microscope fitted with an eyepiece graticule measuring in units of 0.025 mm at maximum magnification. Density of structures was assessed using a 2 × 2 mm square aperture cut in a paper mask. Oil gland structures in the leaf were examined in transmitted light by using the torch (flashlight) function on an inverted standard smartphone e.g. Samsung Galaxy S10, held below a dried herbarium leaf under the dissecting microscope. The drawings were made with the same equipment with a Leica 308700 camera lucida attachment. It was necessary to soak or boil the flowers and fruits to rehydrate them so as to allow dissection and observation of the inner structures of the corolla and androecium. The format of the descriptions and terminology for specialised structures generally follows Beentje (2016) and those in other papers describing new species in *Ardisia* (e.g. Cheek and Xanthos 2012). Measurements were made of stems, leaves, inflorescences, flowers and fruits by using a microscope eyepiece micrometre and a graduated ruler.

In every description the range of measurements is given with the extreme dimensions indicated in parentheses. Provisional conservation assessments were made using the criteria and categories of IUCN (2012) using the required IUCN cell-size of 4 km^2.

RESULTS

Based on the current study of herbarium specimens and related literature, a total of nine creeping herbaceous species of *Ardisia* are recognised in Africa, In addition to the three previously described species, six new creeping species were discovered hiding among specimens collected between 1974 and 1996. Additional taxa were indicated but could not be described due to lack of material or difficult access (see under *Ardisia sadebeckiana* and in discussion). All these species, including the newly described species, appear to be endemic to Gabon and/or Cameroon. A key to these nine species of *Ardisia* is presented below. Treatments of all nine species are presented in alphabetical order, with illustrations and full descriptions and illustrations of all six new species to science and synoptic accounts of the other three species.

Morphological characteristics of herbaceous African Ardisia

The herbaceous species described in this paper differ in several features from other African species of *Ardisia*:

1) Their stems appear not to thicken or to become woody, remaining slender, flexible and have the same diameter as newly formed stems, even 30 cm or more from the stem apex.
2) In all species observed, the older part of the stems appears to be horizontal, running along the surface and rooting, only the apical part curving upwards, becoming aerial and ascending towards the vertical, but never reaching more than about 10 cm above the soil level. The lower nodes of the aerial part develop long adventitious roots that drop to soil level on the side of the stem that is moving forward, pulling the lower aerial nodes towards the ground. This appears to be a continuous process, regulating the height of the stem apex above the ground (keeping it low).
3) Plagiotropic (perpendicular) side shoots, so characteristic of the genus as a whole, with their laterally compressed, triangular bases, are not produced in the African herbaceous species. Inflorescences are borne on the main axis and not on the plagiotropic stems as in most woody African *Ardisia*. Side shoots which root immediately, giving rise to new plants are produced sporadically from the horizontal part of the main axis 15 to 30 cm distant from the apex of the main stem.
4) The leaf phyllotaxy of the primary stem is distichous (in two ranks) not spiralled as in woody African species.
5) Large (comparatively: visible with a 10× hand lens, c. 0.1 mm diam.) peltate, adpressed scales occur on the abaxial surface in most, but not all of the herbaceous species. These are unknown on the leaves in the shrubby species of Africa.

In view of the above marked architectural and morphological separation of these species not only from all other African species of the genus, but those globally, they are here proposed as a separate subgenus:

Kamardisia Cheek, **subgen. nov.**

Type species: *Ardisia ebo* Cheek, Kew Bull. 67: 281. 2012.

Diagnosis

Differing from all other subgenera and species groups of *Ardisia* in: the herbaceous habit (stems not thickening with age), primary stems prostrate or decumbent, rooting adventitiously along their length, with distichous phyllotaxy and absence of plagiotropic branches (not with erect primary stems that become woody, with spiral phyllotaxy and with one or more plagiotropic branches).

Notes

Nine species, comprising three in Cameroon and six new species (this paper) in Gabon (one of these extending to Cameroon). It is possible that these species represent not just a separate subgenus but a distinct genus, apart from *Ardisia*. However, additional data including from pollen and from molecular phylogenetic studies in the context of a global study of the genus is advisable before making this designation formally. For the moment, none of the taxa of this group have been studied for their pollen nor included in any molecular study.

Microstructures as important taxonomic characters in African Ardisia

Oil glands. Taton (1979) was first to draw attention and to illustrate in detail the oil glands in the leaves (and other structures) of African *Ardisia* as valuable taxonomic characters. Features of value at separating species are based on observations in a) reflected light on i) the adaxial and ii) the abaxial surfaces and b) in transmitted light. In some species in reflected light these are invisible, in others black, in others an intermediate state. In transmitted light they are most comprehensively seen and measured accurately.

These structures vary in:

1) Density, (expressed as a number in a 2 × 2 mm square measured between midrib and margin at mid length of a blade).
2) Shape (from orbicular, to elliptic, to linear)
3) Size
4) Uniformity (in some species a reticulation on a blade is typically occupied by a large elliptic oil gland and several much smaller satellite glands)
5) Position (while some species have oil glands scattered evenly through the blade, in others they are present only in the marginal ½ to ¼ of the blade)
6) Prominence (in some species the oil glands appear flat, at the same level as the blade surface, in others they can be raised like a hill)
7) (In transmitted light) colour, varying from colourless, to brown, to red, to black.

Indumentum. The variation in indumentum, primarily on the leaf blade surfaces, matches the variation and taxonomic value of the oil glands. In the herbaceous species two main types of indumentum were observed:

Peltate scales. Usually red in colour (sometimes drying black and then confused with oil glands) these vary in shape and size, and complement (the mixture of scales present), from one species to another. Most Gabonese herbaceous species in this paper have (comparatively) large (0.1 mm diam.) orbicular peltate scales (absent from all Cameroonian species). In some species the scales are bow-tie-shaped (figure of 8), while in others they are Y-shaped, these scales being generally in the range of 0.05 to 0.075 mm diam. Smaller still (<0.05 mm diam.) are trifid, quadrate, stellate, or linear centrally attached (medifixed) structures presumed to be homologous with these scales. These are at the limit of visibility with a normal dissecting microscope. Mixtures of different shapes appear characteristic of some species.

Hairs. These are basally attached, cylindrical, and short or long, simple or branched (sometimes large and stellate with irregular sinuous, filamentous arms).

Glands. Globose red sessile glands characterise some species (e.g. on the pedicels of *A. chaillu*).

Key to the herbaceous species of *Ardisia* Sw. in continental Africa

1. Leaves with red, circular or slightly lobed, peltate scales conspicuous on at least the abaxial leaf-blade (c. 0.1 mm diam., visible with a 10× hand lens) 5

– Leaves lacking circular, peltate scales on the abaxial blade surface (< 0.1 mm diam., not visible with a 10× hand lens) 2

2. Leaves 3–7(–8) cm wide; flowers 3–6 per inflorescence; calyx lobes c. 2 mm long 3

– Leaves (1.5–) 1.9–2.8 cm wide; flowers 2(–3) per inflorescence; calyx lobes 0.7–0.8 mm long .... ***A. ebo***

3. Leaf-blade 5.5– 7(–8) cm wide; base cordate, margin entire .... ***A. sadebeckiana***

– Leaf-blade 3–5 cm wide; base acute, margin crenate 4

4. Petiole 7–10(–18) mm long; leaf-blade discolorous, drying black above, dull white below .... ***A. schlechteri***

– Petiole 3–5(–10) mm long; leaf-blade ±concolorous, drying green on both surfaces .... ***A. massaha***

5. Leaves 4.4–5.3 × 2.1–2.2 cm, apex acuminate ..... ***A. minuta***

– Leaves 4.3–9.3(–12.2) × (2.7–)5–6.3 cm, apex acute or rounded 6

6. Leaf apex broadly rounded, base abruptly cordate .... ***A. ngounie***

– Leaf apex acute, base obtuse or rounded 7

7. Leaves rhombic, the distal ½ to ⅔ with distinct marginal teeth; pedicels glabrous apart from sessile globose, red glands; fruit with 5 longitudinal lines; leaf nervation inconspicuous .... ***A. chaillu***

– Leaves elliptic or ovate-lanceolate, margins entire or sinuous, sometimes with inconspicuous marginal teeth proximally and distally; pedicels with broad, short acute hairs, non-glandular; fruit (where known) lacking longitudinal lines; leaf nervation conspicuous 8

8. Peltate scales present on adaxial as well as abaxial blade surface; leaf length: width ratio <2; secondary and tertiary veins raised, conspicuous on adaxial surface of leaf; calyx lobes about as long as wide .... ***A. hansii***

– Peltate scales present only on abaxial blade surface; leaf length: width ratio >2; secondary and tertiary veins inconspicuous on adaxial surface of leaf; calyx lobes nearly twice as broad as long .... ***A. waka***

TAXONOMIC TREATMENT

Ardisia chaillu P.Peng & Cheek, **sp. nov.** (Figures 1, 2).

Type: Gabon, Ngounié. Massif of Chaillu. Near Mouyanama, about 27 km. E. of Mimongo; alt. ±800 m; 1°39′ S, 11°46′ E; fr. 26 Nov. 1983, *A.M. Louis*, *F.J. Breteler* & *J. de Bruijn 915* (holotype WAG [WAG1113120]).

Diagnosis

Ardisia chaillu differs from *A. hansii* P.Peng & Cheek to which it is similar (in habit, also both have similar leaves with an acute blade apex, and large circular peltate scales on the abaxial leaf surface), by having distinct marginal teeth in the distal ½ to ⅔ of the blade, pedicels glabrous apart from sessile globose glands on the surface (Fig. 1J), pectinate sepal margins, and fruit with 5 longitudinal lines (*Ardisia hansii* has leaves with marginal teeth inconspicuous, pedicels lacking globose glands but with broad, short acute hairs, entire sepal margins, and fruits with no longitudinal lines).

In addition, the leaves of *Ardisia chaillu* are generally larger, in the region of 10 cm long (in *A. hansii* they are generally 4 to 7 cm long and only exceptionally 8 cm) and the oil glands are black, but obscure on the adaxial surface in reflected light, while in *A. hansii* they are conspicuous at the surface, brown and numerous.

Description

Small creeping shrubby herb, forming leafy mats. Stems decumbent, creeping horizontally, terete, 1.75–3 mm diam., internodes 0.4–2.4 cm long, distal part unbranched, erect, c. 20 cm high, producing adventitious roots, new stems arising c. 12 cm apart along the creeping portion, indumentum densely furfuraceous, red-brown in the distal 1–2 cm below the stem apex, then abruptly glabrescent, epidermis grey-brown, longitudinally ridged. Leaves alternate, the blade rhombic, 4.3–10.4 × (2.1–)3.3–4.2 cm, apex acute, (1–)3–4 × 3–4 mm, base acute, often slightly asymmetric, margin revolute, obscurely crenate, crenations (6–)12–16 on each side in the distal ½ – ¾ of the blade, each (0.25–)0.35–0.875 × 2.5–4(–4.75) mm, lateral nerves 12–14 on each side of the midrib, brochidodromous, inframarginal nerve 1.9–3.5 mm from the margin, tertiary nerves coarsely reticulate, raised on adaxial surface, moderately conspicuous; trichomes evenly distributed on the abaxial leaf surface, orbicular peltate scales red (Fig. 1 B), 0.1–0.125 mm diam., 33–39 per 2 × 2 mm, also appearing on the adaxial leaf surface in density of 3–6 per 2 × 2 mm, c. 0.075 mm diam., dark red (Fig. 1 C), adaxial surface otherwise glabrous; suborbicular scales smaller and darker, c. 0.05 mm diam., 3–11 per 2 × 2 mm; oil glands orbicular, elliptic or oblong, appearing dark black in transmitted light, but inconspicuous in reflected light on both surfaces sometimes very slightly raised (but more frequently not and then invisible), 0.1–0.6(–1.13) mm in diam., 7–10 per 2 × 2 mm, flower-shaped scales (with c. 5 radiating obovate arms) clustered on the midrib, red, 0.05–0.075 mm diam., 2–6 per 0.25 × 0.25 mm, slender inclusions visible in the midrib, yellow-orange or dark brown, 0.25–1.38 mm diam.. Petiole plano-convex, (2.5–)4–9(–13) mm long, 0.75–1.25 mm wide, oil glands visible raised strongly at the surface, amber, elliptic, 0.2–0.3 mm diam., indumentum as stem apex. Inflorescences axillary, fasciculate, c. 7 per stem, 1–4-flowered; peduncle suberect, 0.25–0.75 × 0.75–0.88 mm, indumentum as stem apex, bracts 2–3, spatulate (Fig. 1 G), concave, 1.5–2.6(–4) × 0.4–0.75 mm, indumentum as stem apex, bracteoles resembling bracts, 1 × 0.25 mm. Pedicel subcylindrical, 6–8 × 0.5 mm, sessile glands on the surface dark red, 2–4-lobed, tiny irregular, 0.025–0.05 mm diam., 5–8 per 0.25 × 0.25 mm, oil glands visible raised strongly at surface, fulvous, elliptic, 0.125–0.15(–0.2) mm diam., 2–4 per 0.25 × 0.25 mm. Calyx cupular, reflexed on mature fruits, tube 0.25 × 1.25–1.375 mm, lobes 5, overlapping, subtriangular, 0.6 × 0.75–0.88 mm, apex acute, oil glands visible raised strongly at surface, fulvous, elliptic, 0.075–0.18 diam., 3–5 per 0.25 × 0.25 mm, sessile glands (Fig. 1 J) on the surface of pedicels, margin pectinate, lined with simple hairs 0.025–0.125 mm long (Fig. 1 I).

Flowers not seen. *Fruits* (immature) dark green (Fig. 1 F), globose, c. 2–2.625 mm diam., glands visible raised slightly at surface, orbicular to elliptic, pale red in reflected light, 0.1–0.4 mm diam., mature fruits (Fig. 1 H) globose, orange 6–7 mm diam., with 5 pale longitudinal lines (see Fig 1H); glands raised strongly at surface, orbicular to elliptic, 0.275–0.8 mm diam., dark red in reflected light.

Etymology

Ardisia chaillu is named as a noun in apposition for the Chaillu Mountains in southern Gabon (which extend into Republic of Congo) from where the type specimen originates.

Phenology

Fruiting in November.

Distribution and habitat

Endemic to Gabon, near Mouyanama, East of Mimongo. Old secondary, partly primary evergreen forest, alt. ±800 m.

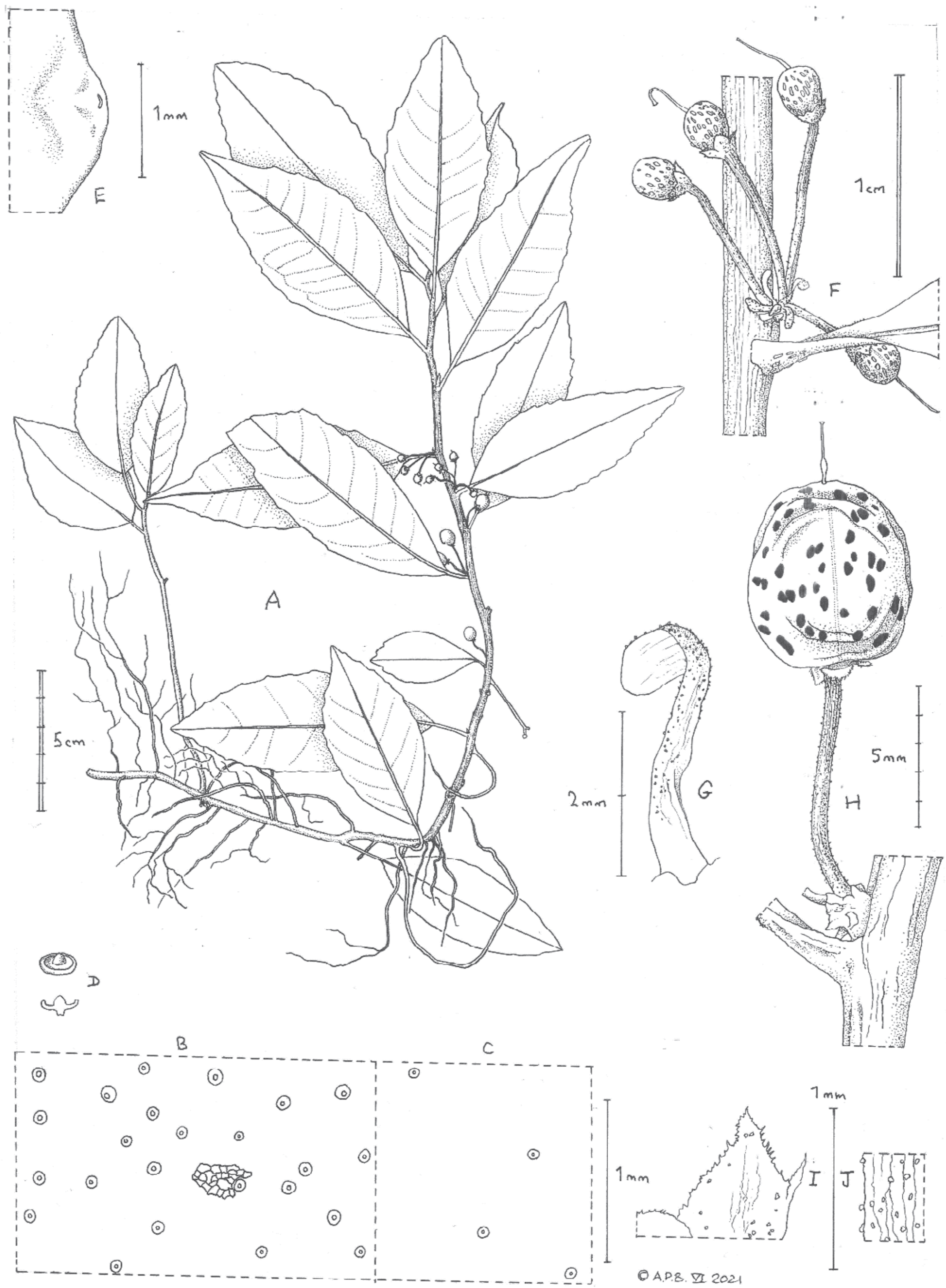

Figure 1. *Ardisia chaillu* P.Peng & Cheek – **A.** habit, whole plant in fruit; **B.** abaxial leaf surface showing peltate scales (orbicular discs) and detail of lower epidermis; **C.** adaxial leaf surface showing peltate scales; **D.** detail of the peltate scale; **E.** adaxial leaf margin showing pore; **F.** node with immature fruits; **G.** spatulate bract; **H.** mature fruit; **I.** sepal showing oil glands and pectinate margin lined with simple hairs; **J.** pedicel surface showing sessile glands. From *A.M. Louis*, *F.J. Breteler* & *J. de Bruijn 915*. All drawn by Andrew Brown.

Figure 2. Holotype of *Ardisia chaillu* P.Peng & Cheek (*Louis et al.* 915 [WAG1113120]).

Conservation status

Only known from the type specimen. Observations on Google Earth (viewed April 2024) at the grid reference given for the type specimen failed to detect any obvious threats at the site, however image resolution was low. We here provisionally assess the species as Vulnerable VU D2 since only a single site is known in an area that appears not formally protected. Other areas in the Chaillu are subject to open cast mining and logging (Cheek pers. obs.) which could well pose a threat to this species in the near future.

Notes

The type specimen had not previously been identified to species (Sosef et al. 2006).

The species is most likely to be confused with *A. hansii* which is geographically disjunct (see diagnosis for differentiating features). Other herbaceous *Ardisia* species in the Chaillu Massif are *A. minuta* and *A. waka*.

Ardisia ebo Cheek, Kew Bull. 67: 281. 2012.

Type: Cameroon, Littoral Region, Ebo Proposed National Park, Yingui Commune, 4°19’ 00” N 10°25’ 40” E; 23 Apr. 2005; fl. fr.; *Cheek* 12503 (holotype K [K000678251]; isotypes WAG, YA).

Diagnostic features

Similar to *A. schlechteri* Gilg, both having elliptic leaves with subacuminate apices, acute to obtuse bases, lacking conspicuous peltate scales, *A. ebo* differing by having concolorous smaller leaves, (1.5)–1.9(–2.8) cm wide, with oil bodies conspicuous, raised on the abaxial surface, calyx lobes 0.7–0.8 mm long. (*Ardisia schlechteri* has discolorous larger leaves, (3.7)–4.2–5 cm wide, oil glands conspicuous, black on the adaxial surface, and c. 2 mm long calyx lobes).

Etymology

Ardisia ebo is named as a noun in apposition for the highly threatened yet species diverse Ebo forest in Littoral Region, Cameroon from where the type and only known specimen originates.

Phenology

Flowering and fruiting in April.

Distribution and habitat

Ardisia ebo appears endemic to the Ebo Forest of Cameroon: Littoral Region, near Yabassi and Yingui, Lowland to submontane evergreen forest; alt. 550 – 800 m. (Cheek and Xanthos 2012).

Conservation status

Only known from the type specimen. Despite several further botanical surveys at Ebo in recent years, no further collections of this taxon have been found. The forest is highly threatened by ongoing logging which may be followed by agriculture. As a result the species is assessed as Critically Endangered (Lovell and Cheek 2020). The Ebo forest contends as one of the important sites for plant conservation in Cameroon and is designated as an Important Plant Area (Murphy et al. 2023). Ebo is globally important for the high number of other published globally unique species of plant, e.g. *Palisota ebo* Cheek (Commelinaceae, Cheek et al. 2018), *Uvariopsis dicaprio* Cheek & Gosline (Annonaceae, Gosline et al. 2022), *Memecylon ebo* R.D.Stone & Cheek (Melastomataceae, Stone et al. 2024), *Begonia ebo* H.Lockwood (Begoniaceae, Lockwood and Tchatchouang 2025). Ebo also has the highest number of Critically Endangered species of all Important Plant Areas in Cameroon since the two last mentioned species take the total to 25, surpassing the Ngovayang massif which has 24 such species (Murphy et al. 2023). Both are extremely important priorities for conservation in Cameroon.

Notes

In the protologue, several other specimens were ascribed to this taxon from further southeast (Cheek and Xanthos 2012), but these have now been segregated as the separate taxon *A. hansii* (see following species in the current paper). *Ardisia ebo* differs from *A. hansii* e.g. in lacking the large (clearly visible with x 10 hand lens) peltate orbicular scales of the abaxial blade. The ranges of the two taxa are separated by about 200 km geographically.

In sharing the absence of large conspicuous peltate scales, and also the general elliptic, crenate, leaf shape, *Ardisia ebo* is also similar to *A. schlechteri,* which is known only from sea level at the coast northwest of Mt Cameroon, about 150 km to the NW of Ebo. *A. schlechteri* differs among other features in having larger leaves which are discolorous, and longer petioles, and in having dense orbicular oil glands that show black on the adaxial blade surface in reflected light (see diagnostic features under *A. schlechteri* below and Table 1).

Comparisons of *A. ebo* in the protologue (Cheek and Xanthos 2012) with *A. schlechteri* and *A. sadebeckiana* (the only other herbaceous *Ardisia* species then known in Africa) are flawed because at that time the second author did not have access to the type and only specimens of either species (in fact the type of the first only came to light recently), and so the characteristics given were based on those in the literature which are misleading since based on other material now known not to be conspecific.

Ardisia hansii P.Peng & Cheek, **sp. nov**. (Figures 3, 4).

Type: Cameroon, South Region. 4 km. on the road from N'Koemvone to 'Akoakas rock'; 2°49′ N, 11°10′ E, fl. fr. 4 Oct. 1974, *J.J.F.E de Wilde 7605B* (holotype K [K000678894]; isotype WAG [WAG1113076]).

Diagnosis

Ardisia hansii differs from *Ardisia chaillu*, to which it is similar (in habit, also both have similar leaves with an acute blade apex, and large circular peltate scales on the abaxial leaf surface), by having leaves with inconspicuous marginal teeth, pedicels with broad, short, acute hairs, lacking globose glands, entire sepal margins, and fruits with no longitudinal lines (*A. chaillu* having distinct marginal teeth in the distal ½ to ⅔ of the blade, pedicels glabrous apart from sessile globose glands on the surface (Fig. 1J), pectinate sepal margins, and fruit with 5 longitudinal lines). In addition, the leaves of *Ardisia chaillu* are generally larger, in the region of 10 cm long (in *A. hansii* they are generally 4 to 7 cm long and only exceptionally 8 cm) and the oil glands are black, but highly obscure on the adaxial surface in reflected light, while in *A. hansii* they are conspicuous at the surface, brown and numerous.

Description

Small creeping herb or subshrub, forming leafy mats. Stems decumbent, creeping horizontally for 30 cm or more, terete, 1.25–2 mm diam., internodes 0.2–3.4 cm long, distal part unbranched, erect, 3.5(–18) cm high, producing adventitious roots, new stems arising 10–15 cm apart along the creeping portion, indumentum densely furfuraceous, red-brown (Fig. 3 B) in the distal 1–2 cm below the stem apex, then abruptly glabrescent, epidermis pale brown, longitudinally ridged. Leaves alternate, elliptic, (2–)4–7.8(–8) × (1.2–)2–3.4(–4) cm, apex acute, 1–5 × 2–4 mm, base acute, often slightly asymmetric, margin revolute, obscurely crenate, crenations 12–16 on each side in the distal ½ – ¾ of the blade, 0.3–0.5(–1) × (2–)3–5 mm (Fig. 3 C), lateral nerves 12–14 on each side of the midrib, brochidodromous, inframarginal nerve 1.5–3.25 mm from the margin, tertiary nerves coarsely reticulate, raised on adaxial surface, moderately conspicuous; trichomes evenly spread on the abaxial leaf surface, orbicular peltate scales (Fig. 3 D) dark brown or dark red, 0.1–0.125 mm diam., 34–41 per 2 × 2 mm, (also appearing on the adaxial leaf surface in density of 2–3 per 2 × 2 mm, which is otherwise glabrous); suborbicular scales smaller and darker, c. 0.05 mm diam., 3–11 per 2 × 2 mm; stellate hairs sparse, interspersed with scales, centre dark red, grading to translucent, towards the distal end, 0.075–0.38 mm diam., 3–5 per 2 × 2 mm, each stellate hair 3–6 armed; cross-shaped scales on the abaxial leaf surface dark red or pale red, 0.075–0.1 mm diam., 3–8 per 2 × 2 mm; oil glands (Fig. 3 D) orbicular, elliptic or oblong, appearing dark black, yellow-orange or colourless in transmitted light, black and inconspicuous in reflected light, not raised or raised very slightly, 0.1–0.625 mm diam., 9–25 per 2 × 2 mm. Petiole canaliculate, 4–13 mm long, 0.5–1.68 mm wide, indumentum as stem apex. Inflorescences axillary, fasciculate, sessile, 2–11 per stem, (1–)3(–4)-flowered; bracts 2–4, narrowly triangular, concave, 0.75–2.25 × 0.25–0.5 mm, stellate hairy (Fig. 3 H), dark brown, 0.05–0.125 mm diam. c. 22 per 0.25 × 0.25 mm. Pedicel curving downwards, subcylindrical, 1.5–7 ×

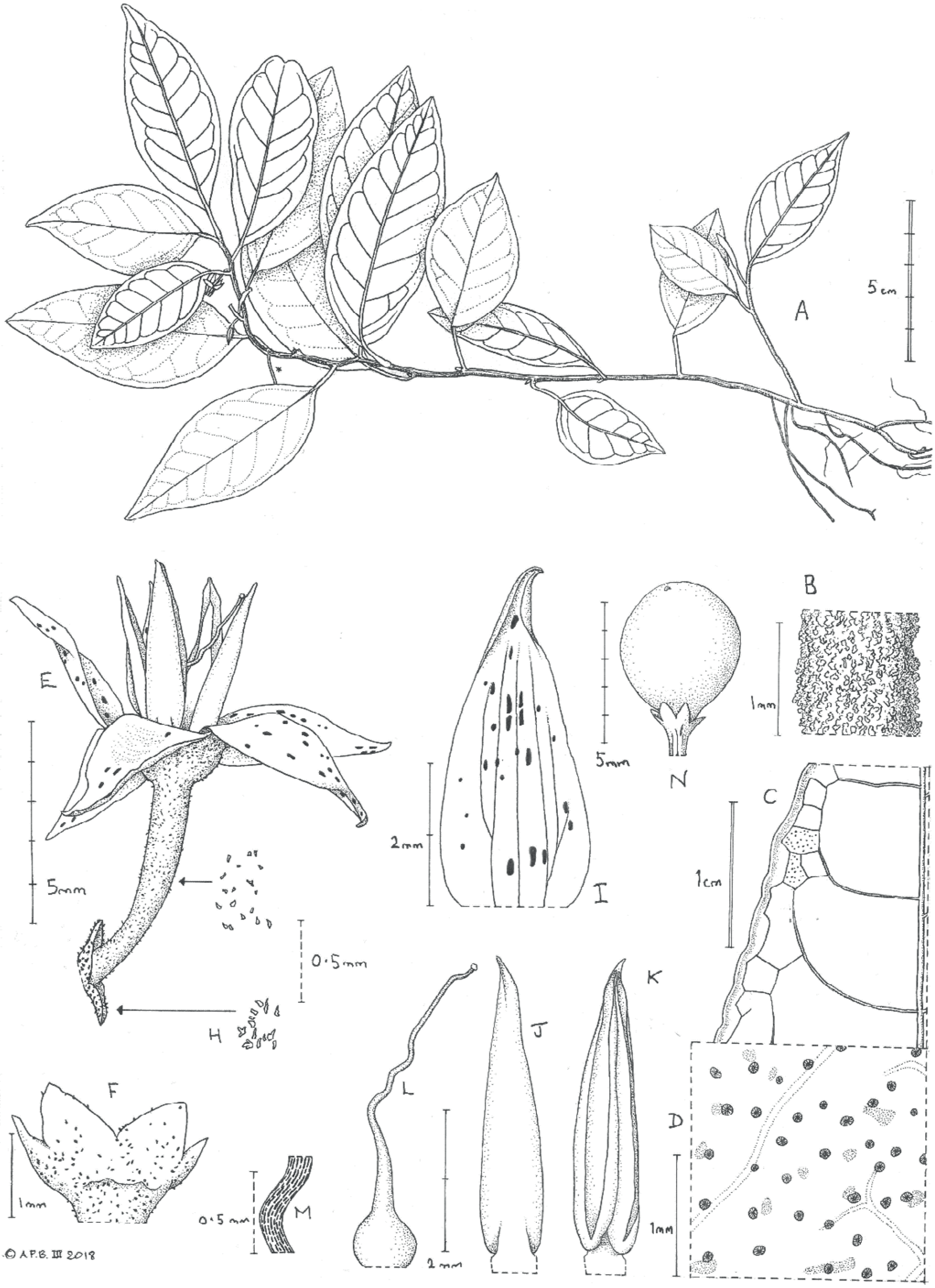

Figure 3. *Ardisia hansii* P.Peng & Cheek – **A.** habit, whole plant in flower, * = adventitious roots; **B.** stem indumentum; **C.** abaxial leaf margin with scales; **D.** abaxial leaf surface showing peltate scales (dark discs) and oil glands (stippled areas); **E.** flower, side view, inverted; **F.** calyx; **G.** indumentum of pedicel; **H.** indumentum of flower bracts; **I.** petal (inner face); **J.** stamen (outer face); **K.** stamen (inner face); **L.** ovary, style and stigma; **M.** detail of style showing parallel pigmented bars; **N.** fruit (immature). [A, C-M. from *J.J.F.E. de Wilde* 8144; B. from *J.J.F.E de Wilde* 7605B; N. from *Breteler* & *J.J. F.E. de Wilde* 573]. All drawn by Andrew Brown.

Figure 4. Holotype of *Ardisia hansii* P.Peng & Cheek (WAG1113076).

0.25–1 mm, oil glands visible, raised strongly at surface or not, ivory or orangish red, suborbicular or oblong, 0.1–0.45 diam., 2–4 per 0.25 × 0.25 mm, indumentum as bracteoles (Fig. 3 G); flower buds oblong, whitish or pale yellow, 2–6 × 1.1–2.1 mm, apex contorted. Calyx (Fig. 3 F) cupular, tube 0.38–0.6 × 1–1.5 mm, lobes 5, subtriangular, 0.5–1 × 0.5–0.75 mm, apex attenuate or acuminate, glands visible raised strongly at surface, ivory or orange, suborbicular, 0.05–0.125 diam., 4–8 per 0.25 × 0.25 mm, indumentum as bracts, margin lined with simple or two-branched hairs of 0.025–0.1 mm long; corolla (Fig. 3 E) spreading, white or pale lilac, lobes (Fig. 3 I) 5, ovate-elliptic, 3.25–5 × 1.38–2 mm, glands visible at adaxial and abaxial surface, ivory or orange, suborbicular or oblong, 0.05–0.45 mm long, 2–4 per 0.25 × 0.25 mm. Androecium yellow, stamens (Fig. 3 J,K) 5, erect, staminal tube present, pale yellow, 0.15 × 0.5 mm, filaments pale yellow, flattened. 0.175 × 0.6 mm, anthers orange in the centre, pale yellow at the margin, introrse, dehiscing by two longitudinal slits, sagittate, 4–4.25 × 0.88–1.25 mm, connective 0.18 × 0.12 mm, pollen pale yellow, hidden in the inner sunken part of the anther; gynoecium (Fig. 3 L) superior, ovary globose, dark red, c. 0.75 × 0.8 mm, style terete, c. 4.2 mm long. Fruit (immature) globose, green (Fig. 3 N), c. 4 mm diam., mature fruits globose, dark red, c. 7 mm diam., glands visible raised strongly at surface, suborbicular, elliptic or oblong, dark red, 0.175–0.65 in diam.

Etymology

The epithet commemorates the collector of the type specimen (and co-collector of all the other specimens known), Dr. Hans (J.F.F.E.) de Wilde of the excellent former Herbarium Vadense at Wageningen, Netherlands. He did much to support Dutch-Gabon botanical co-operation and has been a prolific botanical researcher e.g. of the Meliaceae and Begoniaceae in Africa, collector and teacher, training several competent taxonomic botanists. Many of the new Gabonese species in this paper result from specimens collected by this botanist and his students.

Phenology

Flowering in April and October, buds in November. Fruiting in April and October (immature fruits in September).

Distribution and Habitat

Ardisia hansii occurs in Cameroon and Gabon. In Cameroon at N'kolandom, and also at a site from N'Koemvone to 'Akoakas rock'. In Gabon at Bélinga. Shaded and semi-shaded humid closed high forest, alt. 550–800 m.

Conservation status

The two specimens from Cameroon were collected only about 2 km and less than one year apart. The location in Cameroon at N'kolandom appears to have intact forest canopy (observed on Google Earth April 2025) but has cleared areas only 100 metres distant, and extensive oil palm plantations in the area are increasing in size. The Belinga site is a future open cast iron ore mining site. We calculate an Area of Occupancy of 8 km^2 following the IUCN required cell size, which with the threats and two locations gives a provisional conservation assessment of Endangered (EN B2ab(iii)). The extent of occurrence cannot be calculated as only two points are known.

Notes

The Gabon specimen differs in slight details from the Cameroon specimens e.g. the oil glands appear black and opaque in transmitted light, rather than brown and translucent in the Cameroon material. These specimens were all formerly included within *A. ebo* (Cheek and Xanthos 2012). *Ardisia hansii,* while still rare and restricted, is the most common and widespread of the creeping herbaceous species known so far from Africa, and the only one that is known from more than one country.

Additional material

CAMEROON. South Region: N'kolandom, old secondary vegetation between the village and hill facing the village; alt. ±550 m; 2°48' N, 11°10' E; 5 Apr. 1975; fl. fr.; *J. J. F. E. de Wilde 8144* (K000678252, P04520135, WAG1113077, WAG1113978). **GABON**. Bélinga. Iron mine exploration area; alt. ±750–800 m; 13 Sept. 1978; fl. buds, imm. fr.; *F. J. Breteler* & *J. J. F. E. de Wilde 573* K [K000678893], P [P04520137], WAG [WAG1113080, WAG1113079]).

Ardisia massaha P.Peng & Cheek, **sp. nov.** (Figures 5, 6).

Type: Gabon, Ogooué-Ivindo, about 14 km. along the SOMIFER-road from Bélinga to Makokou. Place called 'Grotte de Massaha' Cave with humid walls of iron ore in shade; alt. ±900–950 m; fr. 18 Sept. 1978, *F.J. Breteler* & *J.J.F.E. de Wilde 707* (holotype WAG [WAG1112951]).

Diagnosis

Differs from *A. ngounie* to which it is most similar (both have 1.55–3.5 mm diam. stems, elliptic leaves, 4.3–12.2 × 2.7–6.3 cm, 8–10 crenations on each side in the distal ½ – ¾ of the blade, 8–10 lateral nerves on each side of the midrib, 3-lobed scales on the abaxial leaf surface and no peltate scales on both adaxial as well as abaxial leaf surfaces), by having an acute apex and base to the leaf-blade, 2-lobed scales on the abaxial leaf surface, no scales on the adaxial leaf surface and archipelago-like oil glands. (*Ardisia ngounie* has an obtuse or rounded, rarely acute leaf-blade apex, a cordate base, 4-lobed scales on the abaxial leaf surface, 3–4-lobed scales on adaxial leaf surface and orbicular or elliptic oil glands).

Description

Small creeping shrublet, forming leafy mats. *Stems* decumbent, terete, 1.9–3 mm in diam., internodes 0.5–1.5 cm long, distal part unbranched, erect 15–18 cm high, producing adventitious roots, new stems arising c. 5 cm apart along the creeping portion, indumentum densely furfuraceous, red-brown in the distal 1–1.5 cm below the stem apex, then abruptly glabrescent, epidermis dark green, longitudinally ridged. Leaves alternate, elliptic, (5.2–)6–9.2(–10.3) × 3–4.9 cm, apex acute, 1–2 × 4–5 mm, base acute, often slightly asymmetric, margin revolute, obscurely crenate, crenations 8–10 on each side in the distal ½ – ¾ of the blade, 0.25–0.5 × 1.5–5 mm, lateral nerves 8–10 on each side of the midrib, brochidodromous, inframarginal nerve 2.5–6.5 mm from the margin, tertiary nerves coarsely reticulate, raised on adaxial surface, moderately conspicuous; trichomes evenly attached to the abaxial leaf surface, 2-lobed scales bowknot-shaped, pale red or red, c. 0.075 mm diam., 6–8 per 2 × 2 mm; 3-lobed scales Y-shaped, pale red or red, 0.075–0.1 mm diam., 10–12 per 2 × 2 mm; oil glands visible on the abaxial leaf surface, orbicular or elliptic, 2 or 3 clustered, dark black, not raised, 0.025–0.225 mm diam., 20–34 per 2 × 2 mm; stellate hairs sparse, interspersed with scales, red, 0.125–0.85 mm in diam., 3–6 per 2 × 2 mm, each stellate hair 2–7-armed, clustered on the midrib of abaxial leaf surface, red, 0.05–0.5 mm diam., 4–8 per 0.25 × 0.25 mm, each stellate hair 3–5-armed (Fig. 5 C). Petiole plano-convex (Fig. 5 B), 3–5(–10) mm long, 0.8–1.35 mm wide. Inflorescences axillary, fasciculate, sessile, 3–5 per stem, 2–4-flowered; bracts 2–4, concave, spatulate, 1–2.25 × 0.6–1 mm, simple or forked hairy (Fig. 5 E), dark red, 0.05–0.12 mm long 5–8 per 0.25 × 0.25 mm bracteoles resembling bracts, c. 1.25 × 0.5 mm. Pedicel curving downwards, subcylindrical, 3–3.2(–8) × 0.25–0.55 mm, stalked glands (Fig. 5 H) visible on the surface, brown, c. 0.05 mm long, 18–24 per 0.5 × 0.5 mm; flower buds elliptic, amber, (1–)1.5–2(–3.2) × 0.75–1.25 mm, apex contorted. Calyx (Fig. 5 G) cupular, tube 0.25–0.4 × 0.6–1.25 mm, lobes 5, ovate, 1.25–1.75 × 0.5–1.25 mm, apex acute, margin lined with simple hairs of 0.05–0.15 mm long. Flower not seen. Fruit (mature) globose (Fig. 5 F), red, 7–9 mm diam., glands visible raised strongly at surface, globose, elliptic or oblong, dark black, 0.15–0.75 diam., 14–19 per 2 × 2 mm.

Etymology

Ardisia massaha is named as a noun in apposition for the place called 'Grotte de Massaha'[Massaha cave], Gabon, from where the type specimen originates.

Phenology

Fruiting in November.

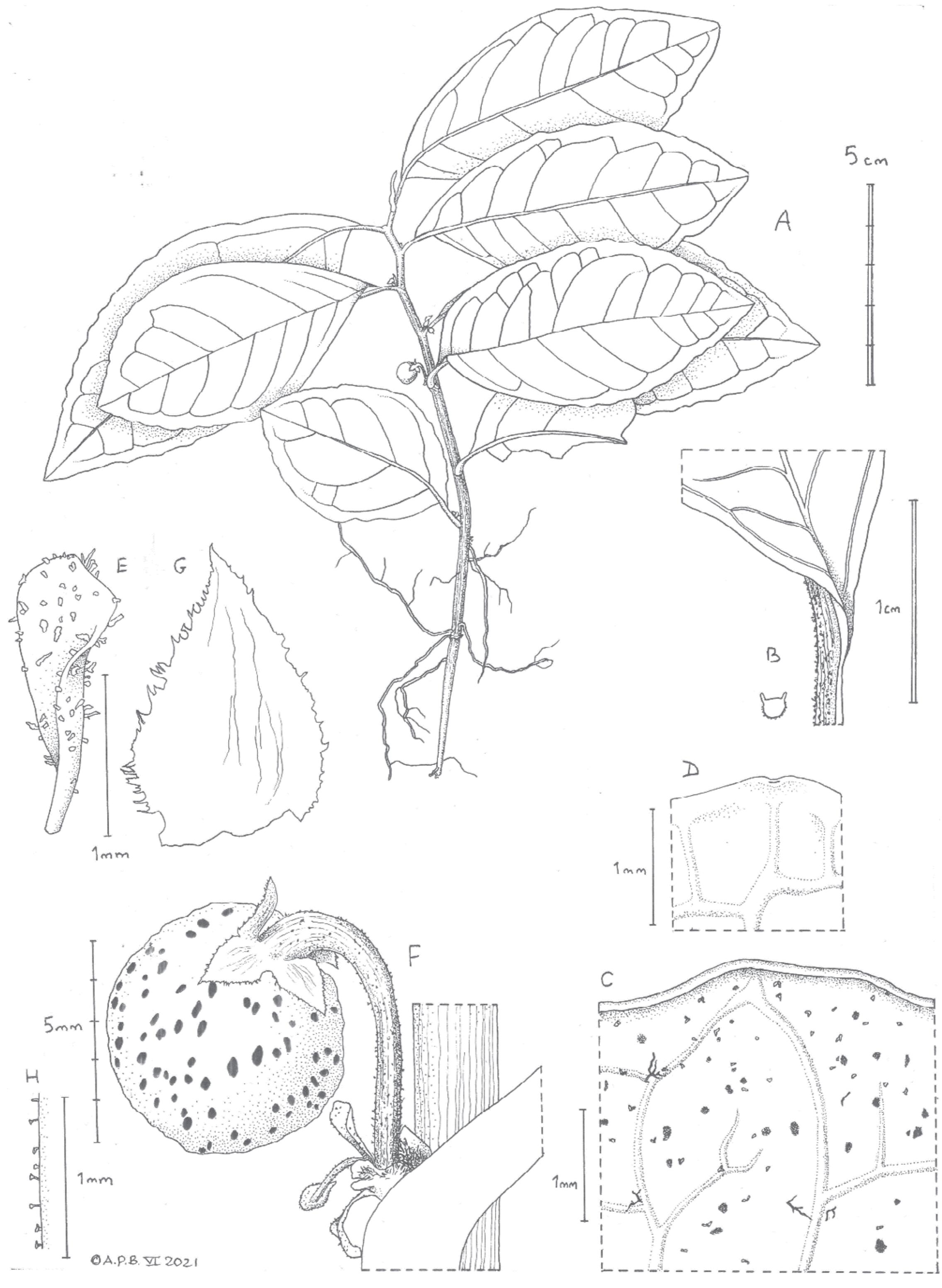

Figure 5. *Ardisia massaha* P.Peng & Cheek – **A.** habit, whole plant in fruit and flower bud; **B.** base of lamina with part of petiole showing plano-convex transverse section; **C.** abaxial leaf surface showing 2/3-lobed scales (smaller irregular trichomes), oil glands (stippled areas) and stellate hairs; **D.** adaxial leaf margin showing pore; **E.** indumentum of spatulate bract; **F.** mature fruit with pedicel, bracts and flower bud; **G.** calyx lobe, outer face; **H.** pedicel surface showing stalked glands. From *F.J. Breteler* & *J.J.F.E. de Wilde 707*. All drawn by Andrew Brown.

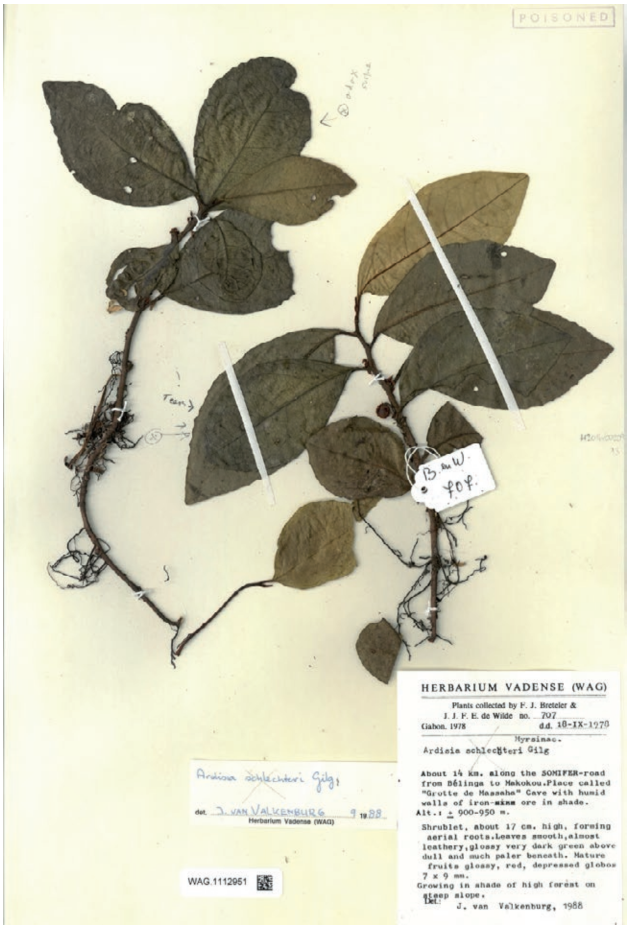

Figure 6. Holotype (WAG) of *Ardisia massaha* P.Peng & Cheek.

Distribution and habitat

Ardisia massaha occurs in Gabon at the Massaha cave on the road from Bélinga to Makokou. Steep slope in cave of iron ore in shade of high forest, alt. ± 900–950 m.

Conservation status

Only known from the type specimen. As the species grows on iron ore, on a road constructed by the former iron ore mining company SOMIFER, iron ore mining directly or indirectly may pose a threat to this species. We calculate the area of occupancy as 4 km^2 using the required IUCN gridcell size, and as there is a single location the provisional assessment is Critically Endangered (CR) B2ab(iii). Iron ore mining at Belinga has been controversial and is of concern for the likely negative consequences for biodiversity conservation (Tzinieris 2014). Future environmental impact surveys for the Belinga iron ore mine should take this species into account.

Notes

The specimen had previously been identified as *A. schlechteri*, which is endemic to the base of Mt Cameroon in SW Region, Cameroon. Please see the key for differences. The other herbaceous *Ardisia* species from Belinga is *A. hansii.*

Ardisia minuta P.Peng & Cheek, **sp. nov.** (Figures 7, 8).

Type: Gabon, Ngounié. Mouyanama, slope of Mount Ngondo, fr. 8 Mar. 1984, *A.M. Louis 1460* (holotype WAG [WAG1113081]; isotype LBV n.v.).

Diagnosis

Ardisia minuta differs from all other herbaceous species in the minute dimensions of its stature (c. 5 cm tall) and its minute leaf blades (the largest reaching 5.3 cm long). Otherwise it is similar to *Ardisia hansii* (both have small leaves, an acute or acuminate leaf apex, stems <2 mm diam. and 0.1–0.125 mm diam. orbicular peltate scales on the abaxial leaf surface), differing by the orbicular peltate scales 7–8 per 2 × 2 mm on adaxial leaf surface and erect pedicels with sessile glands. (*Ardisia hansii* has orbicular peltate scales 2–3 per 2 × 2 mm on the adaxial leaf surface and downward curved pedicels with simple hairs).

Description

Small creeping herb, probably forming leafy mats. Stems decumbent, creeping horizontally, terete, (0.9–) 1.3–2 mm diam., internodes 2–12 mm long, distal part unbranched, erect c. 5 cm high, producing adventitious roots, indumentum densely furfuraceous, red-brown in the distal c. 1.25 cm below the stem apex, then abruptly glabrescent, epidermis dark green, longitudinally ridged. Leaves alternate, elliptic, 4.4–5.3 × 2.1–2.2 cm, apex acuminate, 0.05–0.08 × 0.05–0.08 cm, base acute, often slightly asymmetric, margin revolute, obscurely crenate, crenations 6–8 on each side in the distal ½ – ¾ of the blade, 0.5–0.75 × 2.75–4.75 mm, lateral nerves 8–10 on each side of the midrib, brochidodromous, inframarginal nerve 1–2.4 mm from the margin, tertiary nerves coarsely reticulate, raised on adaxial surface, moderately conspicuous; trichomes evenly attached to the abaxial leaf surface, orbicular peltate scales (Fig. 7 D) red, 0.1–0.125 mm diam., 35–41 per 2 × 2 mm, (also appearing on the adaxial leaf surface (Fig. 7 E) in density of 7–8 per 2 × 2 mm, 0.075–0.1 mm diam., dark red, otherwise glabrous); suborbicular scales smaller and darker, c. 0.05 mm diam., 6–11 per 2 × 2 mm, stellate hairs sparse,

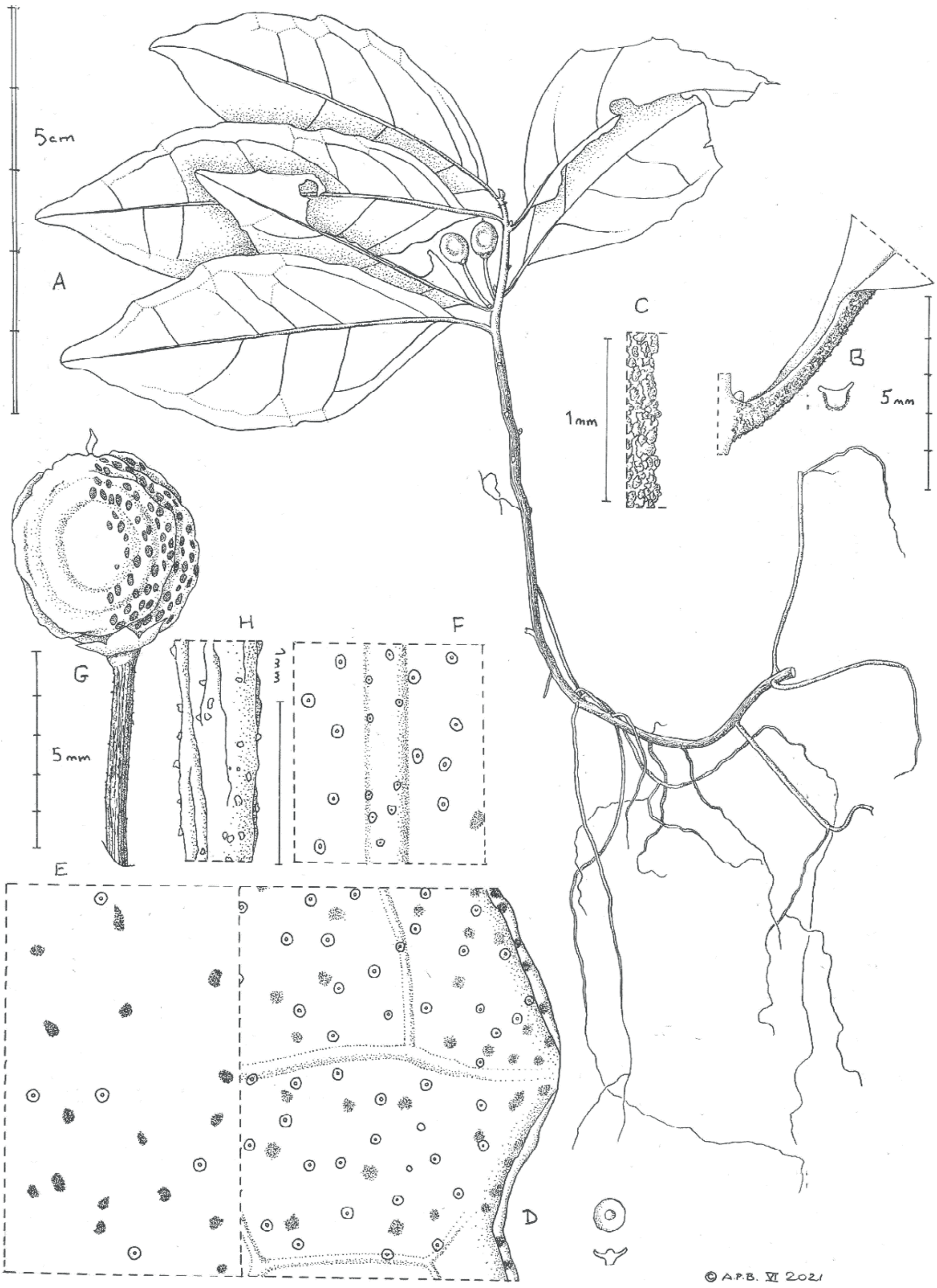

Figure 7. *Ardisia minuta* P.Peng & Cheek – **A.** habit, whole plant in fruit; **B.** base of lamina with part of petiole showing transverse section plano-convex; **C.** indumentum of petiole abaxial surface; **D.** abaxial leaf surface showing peltate scales (orbicular discs) and oil glands (stippled areas); **E.** adaxial leaf surface showing peltate scales (orbicular discs) and oil glands (stippled areas); **F.** abaxial leaf surface with midrib showing flower-shaped scales on the midrib surface and peltate scales on the leaf surface; **G.** mature fruit showing oil glands; **H.** pedicel surface showing sessile glands. From *A.M. Louis 1460*. All drawn by Andrew Brown.

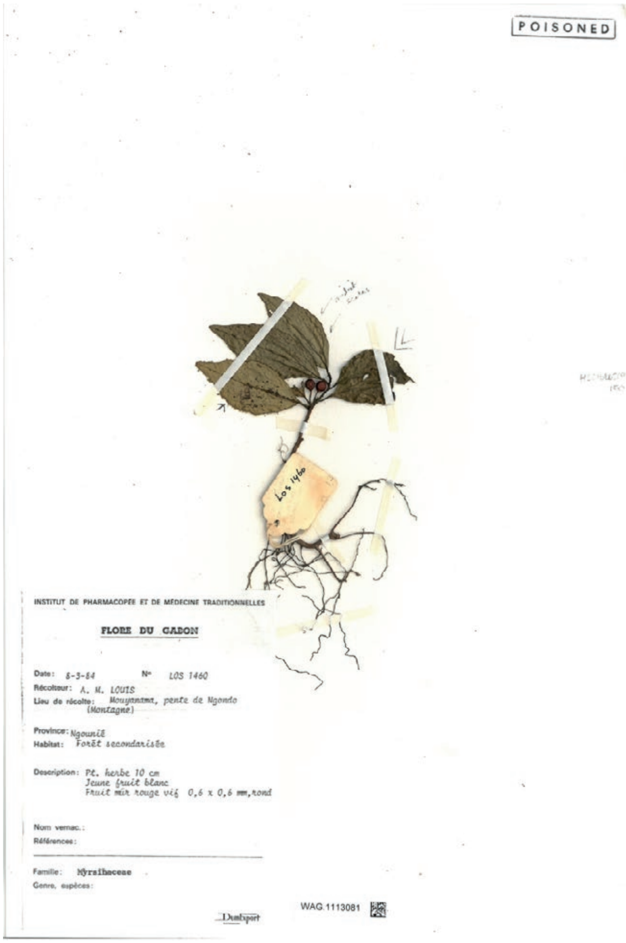

Figure 8. Holotype of *Ardisia minuta* P.Peng & Cheek (WAG).

interspersed with scales, 0.1–0.23 mm diam., 1–3 per 2 × 2 mm, each stellate hair 3–4 armed flower-shaped scales (Fig. 7 F) on the midrib of abaxial leaf surface red, 0.05–0.075 mm diam., 5–10 per 0.25 × 0.25 mm, slender inclusions in the midrib raised slightly, elliptic to oblong, yellow, 0.15–0.4 mm diam., 1–2 per 0.25 × 0.25 mm, oil glands (Fig. 7 D) visible raised strongly at abaxial leaf surface, suborbicular to elliptic, appearing dark black in transmitted light, 0.075–0.35 mm diam., 13–20 per 2 × 2 mm. Petiole plano-convex (Fig. 7 B), (1.5–)4–5 mm long, 0.5–0.9 mm wide. Inflorescences axillary, fasciculate, c. 3 per stem, 2-flowered; peduncle suberect, c. 0.25 × 0.625 mm, indumentum as stem apex, bracts 2, narrowly subtriangular, concave, c. 0.5 × 0.45 mm, indumentum as stem apex, bracteoles resembling bracts, 0.75–1 × 0.25–0.3 mm, indumentum as stem apex. Pedicels erect, subcylindrical, 5.5–5.75 × 0.38–0.45 mm, sessile glands (Fig. 7 H) on the surface dark red, irregular, minute, 0.025–0.05 mm diam., 5–8 per 0.25 × 0.25 mm. Calyx cupular, tube c. 0.25 × 1.25 mm, lobes 5, overlapping, subtriangular, c. 0.625 × 1 mm, apex acute, glands visible, raised strongly at surface, fulvous, elliptic, 0.075–0.15 diam., 3–5 per 0.25 × 0.25 mm, margin lined with simple hairs 0.075–0.125 mm long. Flower not seen. *Fruit* (immature) globose, white, mature fruit red in reflected light, globose, c. 6 mm diam., oil glands (Fig. 7 G) visible, raised slightly at the surface, suborbicular to elliptic, red, 0.1–0.625 mm diam., 30–33 per 2 × 2 mm.

Etymology

The epithet, treated as an adjective in apposition, is derived from the Latin *'minuta'*, which means small. The name refers to the small leaves, stems and upright stems of this species which are all smaller than those of all other species of African *Ardisia*.

Phenology

Fruiting in March.

Distribution and Habitat

Ardisia minuta is endemic to the Chaillu Massif of Gabon: Ngounié, Mouyanama, slope of Mount Ngondo. Secondary forest.

Conservation status

Only known from the type specimen. *Ardisia chaillu* is also recorded from the same area (slopes of Mt Mouyanama in the Chaillu massif) where it was collected a few months earlier by the same collector A.M. (Ard) Louis. No detailed locality data was given for the only known specimen so we can only deduce that as for the aforementioned species that there are no obvious immediate threats at the site. We here provisionally assess the species as Vulnerable VU D2, since only a single site is known in an area that appears unprotected. Other areas in the Chaillu are subject to open cast mining and logging (Cheek pers. obs.) which could pose an imminent threat to *Ardisia minuta* in the near future.

Notes

Ardisia minuta is easily the smallest known African *Ardisia* species.

Ardisia ngounie P.Peng & Cheek, **sp. nov.** (Figures 9, 10).

Type: Gabon, Ngounié, along a forestry road W of Bembodié; 1°28.8′ S, 10°28.4′ E, fr., 27 Oct. 1994, *J.J. Wieringa 2938* (holotype WAG [WAG1113216]; isotypes WAG [WAG1112947], LBV n.v.)

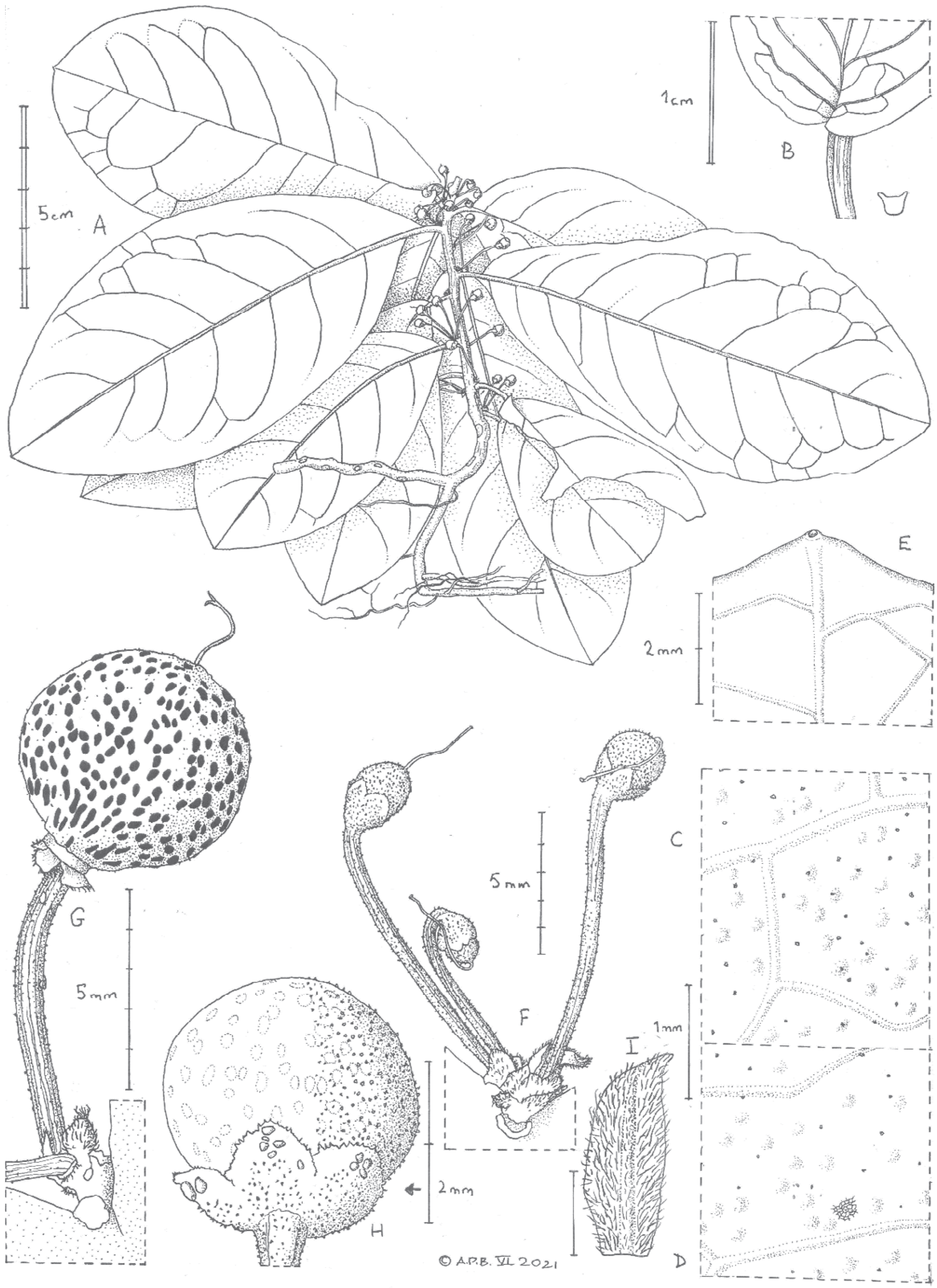

Figure 9. *Ardisia ngounie* **A.** habit, whole plant in fruit; **B.** base of lamina with part of petiole showing transverse section plano-convex; **C.** abaxial leaf surface showing 3-/4-lobed scales (smaller irregular trichomes) and oil glands (stippled areas); **D.** adaxial leaf surface showing 3/4-lobed scales (smaller irregular trichomes), oil glands (stippled areas) and detail of upper epidermis; **E.** adaxial leaf margin showing pore; **F.** immature fruits; **G.** mature fruit; **H.** mature fruit showing details of calyx; **I.** indumentum of bract. A–F-, H, I. from *J.J. Wieringa 2938*; G. from *J.J.F.E de Wilde 11744*. All drawn by Andrew Brown.

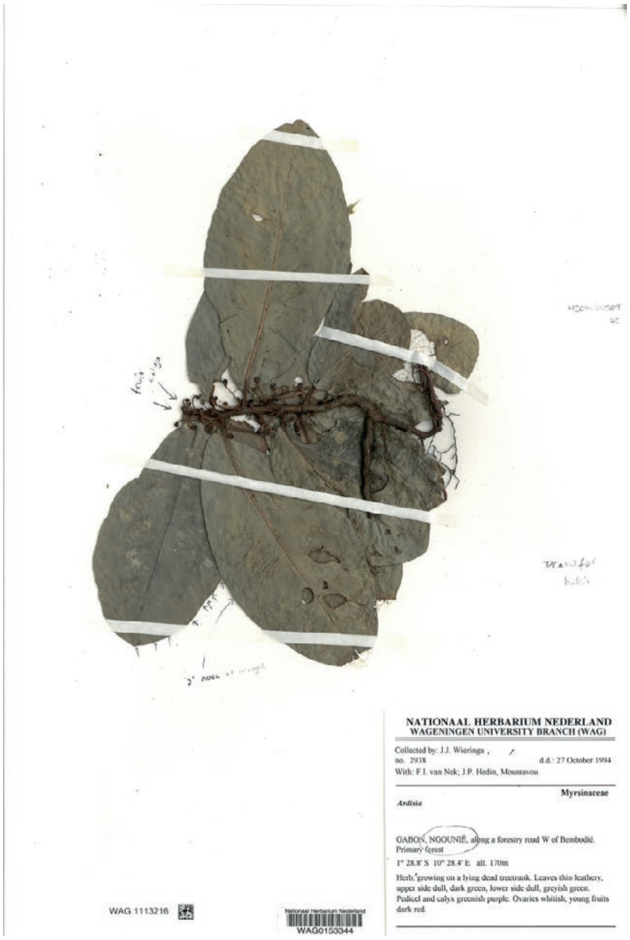

Figure 10. Holotype of *Ardisia ngounie* P.Peng & Cheek (WAG1113216).

Diagnosis

Ardisia ngounie is not likely to be confused with any other in Africa since it alone appears to be fully procumbent, the stem apex not ascending but remaining prostrate. *Ardisia ngounie* is further distinct in the rather thick leaf blades which are rounded to obtuse at the apex and subcordate at the base.

Description

Small creeping herb, probably forming leafy mats. Stems (including apex) procumbent, terete, 1.55–2.9(–3.5) mm diam., internodes 0.3–0.6 cm long, distal part unbranched, erect 9–12 cm high, producing adventitious roots, indumentum densely furfuraceous, red-brown in the distal 1–1.5 cm below the stem apex, then abruptly glabrescent, epidermis dark green, longitudinally ridged. Leaves alternate, coriaceous, elliptic, rarely slightly obovate-elliptic, 4.3–9.3(–12.2) × (2.7–)5–6.3 cm, apex obtuse or rounded, base cordate, often slightly asymmetric, margin revolute, obscurely crenate, crenations 8–10 on each side in the distal ½ – ¾ of the blade, 0.45–0.75 × 3.5–7 mm, lateral nerves 8–10 on each side of the midrib, brochidodromous, inframarginal nerve 1.5–5.25 mm from the margin, tertiary nerves coarsely reticulate, raised on adaxial surface, moderately conspicuous; trichomes evenly attached to the abaxial leaf surface, 3-lobed scales Y-shaped, pale red, red or dark red, 0.05–0.075 mm diam., 4–9 per 2 × 2 mm, 4-lobed scales cruciform or chromosome-shaped, pale red, red or dark red, 0.05–0.075 mm diam., 9–22 per 2 × 2 mm (Fig. 9 C), (also appearing on the adaxial leaf surface (Fig. 9 D), pale red or red, 3-lobed scales Y-shaped, 0.04–0.075 mm diam., 2–6 per 2 × 2 mm, 4-lobed scales cruciform, 0.0375–0.05 mm diam., 8–12 per 2 × 2 mm, which is otherwise glabrous); stellate hairs sparse, interspersed with scales, red, 0.1–0.65 mm in diam., 1–4 per 2 × 2 mm, each stellate hair 3–5-armed, clustered on the midrib of abaxial leaf surface, red, 0.28–0.42 mm diam., 1–4 per 0.25 × 0.25 mm; oil glands (Fig. 9 C) visible on the abaxial leaf surface, orbicular or elliptic, appearing brown in transmitted light, black and inconspicuous in reflected light, strongly raised, 0.125–0.25(–0.38) mm in diam., 74–85 per 2 × 2 mm. Petiole plano-convex (Fig. 9 B), 3–10 mm long, 0.85–2.5 mm wide, indumentum as stem apex. Inflorescences axillary, fasciculate, sessile, 2–13 per stem, 1–3-flowered; bracts 4, spatulate, concave, 1.5–2.25 × 1–1.25 mm, midrib thick raised, dark red, indumentum as stem apex (Fig. 9 I); bracteoles resembling bracts, 3, c. 1.5 × 1 mm. Pedicel curving downwards, subcylindrical, 6–11 × 0.25–0.75 mm, sessile glands on the surface pale red or red, 2 or 3 lobed, c. 0.05 mm in diam., 10–12 per 0.25 × 0.25 mm. Calyx (Fig. 9 H) cupular, tube 0.25–0.375 × 1.25–1.75 mm, lobes 5, inner thicker, dark brown, outer scarious, thinner, pale brown, shallow or not, overlapping, reflexed or not, subtriangular, 0.625–0.75 × 0.75–1 mm, apex acute, oil glands visible on the surface, pale brown, 0.05–0.075 mm in diam., margin lined with simple or forked hairs of 0.1–0.125 mm long. Corolla scar conical frustum-shaped, pale brown, c. 0.2 × 1.7 mm. Flower not seen.Fruit (immature) globose (Fig. 9 F), dark red, (0.875–)1.375–2.25(–3) mm in diam., mature fruits (Fig. 9 G) globose, red, 7–9 mm in diam., glands visible raised strongly at surface, suborbicular, elliptic or oblong, dark black, 0.15–0.675 mm in diam., 14–19 per 2 × 2 mm.

Etymology

Ardisia ngounie is named as a noun in apposition for the Ngounié Province, Gabon from where the type specimen originates

Phenology

Fruiting October and December.

Distribution and habitat

Ardisia ngounie appears restricted to the lower western slopes of the Koumounabouali Massif in the Ngounié Province, south of the lower reaches of the Ogooué River, Gabon. It occurs in primary evergreen forest, alt. 170–350 m.

Conservation status

The two known specimens were collected about 18 km apart, both in the lower western slopes of the Massif of Koumounabouali which reaches 800 m alt.,. The area is unprotected and appears to be logged, in fact one of the specimens was reported as being accessed from a logging road. While logging in Gabon is usually well managed and sustainable, it nevertheless can pose threats to highly local plant species such as this species. This is because log-loading areas and logging trails can destroy the habitat in which they have been placed by the soil compaction and clearance necessary to form them. However, these threats are not considered likely to kill imminently all the plants of the species, so therefore we provisionally assess the species as VU (Vulnerable) D2.

Notes

Both specimens had not previously been identified to species (Sosef et al. 2006). The species is not likely to be confused with any other since it alone appears to be fully procumbent, the stem apex not ascending but remaining prostrate. *Ardisia ngounie* is further distinct in the rather thick leaf blades which are rounded to obtuse at the apex and subcordate at the base. No other herbaceous *Ardisia* is known to be sympatric, but *A. waka* occurs in the Waka National Park, only c. 50 km to the east.

Additional material

GABON. Ngounié, Massif of Koumounabouali; 1°19.6′ S, 10°26.9′ E; alt. 350 m; fr., 11 Dec. 1996, *J.J.F.E de Wilde 11744* (WAG1112947).

Ardisia sadebeckiana Gilg, Bot. Jahrb. Syst. 30: 97. 1901.

Type: Cameroon, South Region, S of Kribi, Grand Batanga; fl. 22 Oct. 1890, *M. Dinklage 902* (lectotype HBG [HBG509261], designated here; isolectotype: HBG [HBG509262]).

(≡) *Afrardisia sadebeckiana* (Gilg) Mez in H.G.A. Engler (ed.), Pflanzenr., IV, 236: 187. 1902.

Diagnostic characters

Ardisia sadebeckiana is a particularly distinct species among the four species (*A. ebo, A. schlechteri, A. massaha*) which lack large, conspicuous peltate scales on the abaxial leaf blade. It is the only one with leaves >5 cm wide, and is further separated due to the obovate leaves with a short mucro at the otherwise rounded apex (the other species having more or less elliptic leaves which are acuminate or subacuminate), the base is abruptly cordate (versus acute). The erect part of the stem is the most pronounced of all the herbaceous species, and this species appears the closest in the group to being a `subshrub'.

Etymology

The name means “in honour of (or to the glory of) Sadebech, presumably for Dr Richard Sadebach, director of the botanical museum of Hamburg whose death was reported in 1905 (Anon. 1905).

Phenology

Flowering in October.

Distribution and habitat

Ardisia sadebeckiana is only known from Cameroon, in the South Region at Grand Batanga just to the south of the city of Kribi. Lowland evergreen forest at sea-level near the coast.

Conservation status

For the moment *Ardisia sadebeckiana* is only known with certainty from the type specimen of which two duplicates survive at HBG. This was collected during the German Colonial Period (1884–1916) when Grand (Gross) Batanga was a major port for Cameroon, close to the now larger port of Kribi. It is remarkable that the species appears not to have been seen since, despite the Kribi area having been a major botanical collection centre, especially in the 1970s and 1980s thanks to the efforts of the staff of Herbarium Vadense (WAG) who had a base there at the former herbarium KRIBI funded by Tropenbos. During this time many new species to science were brought to light including several of those in this paper. This suggests that *Ardisia sadebeckiana* may be/have been highly range-restricted to the former forests of Grand Batanga itself which have been heavily cleared or otherwise impacted by humans over the last 100 years. We urge that attempts are made to refind this species, and should it be rediscovered, measures should be put in place to support its survival, such as a public education campaign.

In recent decades all coastal forest up to c. 2.5 km from the sea has been replaced by palm oil plantations, and much of that which survives has been urbanised, or cleared as log parks (storage depots for timber for export). Therefore, we assess the species provisionally here as Critically Endangered (Possibly Extinct) CR (PE) B2ab(iii) since only a single site (AOO 4 km^2) with major and ongoing threats was recorded 135 years ago. However, the species has not been the subject of targeted searches so it cannot be certain that it is extinct and it may yet survive in a small intact fragment of its habitat. However, other species at Grand Batanga are also feared extinct, such as *Ledermanniella batangensis* (Engl.) C. Cusset (Ghogue 2010) at the Lobé Falls, the most species-diverse site (10 species) for Podostemaceae in Africa (Cheek et al. 2017).

Notes

Of the two sheets at HBG we select as lectotype that barcoded HBG509261 since this bears both the original handwritten field label in Dinklage's hand, and also a label which the author of the name, Gilg, has written the name *Ardisia sadebeckiana*, dating it 1898, four years before his protologue was published.

Ardisia sadebeckiana is the first collected of all the African herbaceous *Ardisia* species and with *A. schlechteri,* the first to be published (Gilg 1902).

Although the species was described from Cameroon, the name *Ardisia sadebeckiana* has been applied to many specimens of prostrate herbaceous species of *Ardisia* collected in Gabon. The situation was not helped by de Wit's (1958) neotypification of the name onto an erect species in that country. This strange error was highlighted in the annotations by Taton on de Wit's neotype. But then Taton himself, in preparation for his magnum opus (Taton 1979) determined specimens from Gabon of another, albeit similar, taxon as *Ardisia sadebeckiana*. These differ from the type e.g. in having dentate, concolorous leaves (vs entire, discolorous leaves). Among the specimens named as this taxon in various herbaria there are likely several additional novel taxa which we intend to describe once we can arrange for a loan. Some of the material described in this paper as new to science, e.g. *Ardisia massaha*, had previously been identified as *A. sadebeckiana.*

Ardisia schlechteri Gilg, Bot. Jahrb. Syst. 30: 97. 1901 (Figures 11, 12).

Type: Cameroon, South West Region, Mt Cameroon, Bibundi, fl., April 1899, *Schlechter 12417* (holotype B, destroyed n.v.; lectotype Z [Z-000088438], designated here).

(≡) *Afrardisia schlechteri* (Gilg) Mez in H.G.A. Pflanzenr., IV, 236: 185. 1902.

Diagnostic features

Ardisia schlechteri is similar to *A. ebo,* both having elliptic leaves with subacuminate apices, acute to obtuse bases, the abaxial surface lacking conspicuous peltate scales. *Ardisia schlechteri* has discolorous larger leaves, (3.7)–4.2–5 cm wide, oil glands conspicuous, black on the adaxial surface, and c. 2 mm long calyx lobes, while *A. ebo* differs by having concolorous smaller leaves, (1.5)–1.9(–2.8) cm wide, with oil bodies conspicuous, raised on the abaxial surface, calyx lobes 0.7–0.8 mm long.

Etymology

Named for the collector of the type and only specimen of this species, Rudolf Schlechter (1872–1925), a prodigious field collector of herbarium specimens in the tropics and also a prolific and expert publisher of taxonomic research at B in many plant families.

Distribution and habitat

Ardisia schlechteri is known from Bibundi, Cameroon, on the coast of Mt Cameroon in the SW Region:

Table 1. Diagnostic characters separating *Ardisia schlechteri* and *A. ebo*. Data taken from the specimens cited in this paper.

	Ardisia schlechteri	*Ardisia ebo*
Leaf blade dimensions	(5.8–)7–9.5 x (3.7–)4.2–5 cm	(2.8–)4.7–6.5 x (1.5–)1.9–2.8 cm
Leaf blade colour	Discolorous, upper surface drying blackish green, abaxial surface off white.	Concolorous, both surfaces more or less green
Adaxial blade surface	Oil glands numerous, dense, black in reflected light	Oil glands not visible in reflected light
Abaxial surface	Oil glands not visible in reflected light	Oil glands conspicuous in reflected light, raised
Petiole length (cm)	0.7–1.2(–1.8)	0.4–0.8

Figure 11. *Ardisia schlechteri* Gilg - **A.** habit, whole plant with flower buds; **B.** adaxial leaf-blade surface near midrib showing dense black oil glands (not coloured) visible in reflected light; **C.** abaxial leaf-blade surface near margin showing sparse black oil glands (not coloured) visible in reflected light; **D.** flower bud, rehydrated; **E.** sepal, outer surface with oil glands (coloured); **F.** petal, outer surface with oil glands; **G.** pistil; **H.** stamen, adaxial face. All drawn from *Schechter* 12417 (lectotype Z) by Andrew Brown.

only known from the type collection cited above. Lowland evergreen forest sea-level at the coast.

Conservation status

The first conservation assessment of *Ardisia schlechteri* was as Critically Endangered (CR) A1c+2C (Cable and Cheek 1998) using the previous IUCN notation, when the species was already considered possibly extinct. This assessment was maintained in Cheek and Cable (2000b) and also in the Red Data Book of the Plants of Cameroon (Onana and Cheek 2011). The species was not found in the intensive botanical surveys of c. 1991 to 1995 that were focussed on prioritisation for conservation of plant species around Mt Cameroon (see Cheek and Cable 1997). The surveys included the only site known for the species, Bibundi, a small fishing village encroached by oil palm plantations initiated in the colonial era, probably soon after Schlechter's visit, which may have rendered this species extinct. The second author has spent time botanising in the Bibundi area in 1995 but failed to refind this species.

Botanical surveys that have been carried out subsequently in other forest areas in S W Region Cameroon and adjoining regions since 1991 (Cheek et al. 1992; Cheek et al. 1996; Cable and Cheek 1998; Cheek et al. 2000; Maisels et al. 2000; Chapman and Chapman 2001; Harvey et al. 2004; Cheek et al. 2004; Cheek et al. 2006; Cheek et al. 2010; Harvey et al. 2010; Cheek et al. 2011) have resulted in over 40,000 specimens and produced over 100 new species to science, but no further records of *A. schlechteri*. Further searches especially at Bibundi are advisable to target this species in the unlikely case that it survives, so that it might then be protected from extinction.

Other lowland forest species collected by Schlechter at Mt Cameroon at the same time as he collected *Ardisia schlechteri* that are now considered extinct are *Oxygyne triandra* Schltr. (Thismiaceae, Cheek et al. 2018; Cheek and Williams 1999) and *Afrothismia pachyantha* Schltr. (Afrothismiaceae, Cheek et al. 2019; 2024).

Notes

What was considered the only known specimen of this species was destroyed at B in 1943 (Taton 1979) until in 2022 we found the previously unknown isotype at Z (Fig. 12) by searching through gbif.org, see https://www.gbif.org/occurrence/2575329283.

Since the Z duplicate is original material and matches the protologue we select it here as lectotype. For the moment is the only material known. It consists of three short aerial stems, one of which bears flowers. It is possible that additional duplicates will be found.

Figure 12. Lectotype of *Ardisia schlechteri* Gilg (Z barcode 000088438).

The only known figure of this species (Fig. 11) was made from the Z specimen while on loan to K. Since there is so little material, we did not rehydrate and dissect the flower bud for fear of damage.

Taton (1979) without having seen the type, already had stated that Hepper's (1963) conjecture that *Olorunfemi* in FHI 30692 might be considered this species was unlikely, and this is beyond doubt now that the type has been seen. Several other specimens from Cameroon and even Gabon have also been identified as this species, some of them also prostrate herbaceous species, but all of them that we have seen are non-conspecific. In Sosef et al. (2006) two specimens are identified as *Ardisia schlechteri,* these are *Breteler* & *J.J.F.E. de Wilde 707* (type of *A. massaha,* described above) and *Louis* 1852 at LBV which we have not been able to access or view.

Ardisia waka P.Peng & Cheek, **sp. nov.** (Figures 14, 15).

Type: Gabon, Ngounié. Old forest along exploitation road, km 2 SE of Forestry Camp Waka, situated about 32 km SE of Sindara, 1 14 S, 10 53 E, Waka River basin. alt. ±300–400 m, fl., 10 Dec. 1983, fl. *A.M. Louis*, *F.J. Breteler* & *J. de Bruijn 1251* (holotype K [K000593393]; isotypes WAG [WAG1113113], LBV n.v.).

Diagnosis

Ardisia waka is similar to *A. chaillu* in having large (>0.1 mm in diam.) peltate scales on both adaxial and abaxial blade surfaces, leaves of similar size, and in the globose sessile glands on the pedicels, but differs in the broadly elliptic leaves with apex acute, obscurely crenate leaves with oil glands sparse and very inconspicuous in the marginal ¼ of the leaf blade (vs lanceolate, acuminate, conspicuously crenate, with black oil glands, conspicuous in both reflected and transmitted light throughout the width of the blade in *A. chaillu*).

Description

Small creeping shrublet, c. 10 cm tall. Stems decumbent, terete, 1.6–2.5 mm diam., producing adventitious roots from basal leaf axils, internodes 0.3–2 cm long, distal part unbranched, oil glands visible in the most distal internode, suborbicular or elliptic, appearing black in reflected light, 0.075–0.15 mm diam., 2–3 per 0.25 × 0.25 mm, erect, indumentum densely furfuraceous, red in the distal 1.5–2 cm below the stem apex, then abruptly glabrescent, epidermis dark green, longitudinally ridged. Leaves alternate, distichous, broadly elliptic, (5.2–)8.2–11 × 3–6.1 cm, apex acute to subacuminate, base acute, often slightly asymmetric, margin revolute, obscurely crenate, crenations 6–8 on each side in the distal ½ – ¾ of the blade, each 0.4–1 × 5–6.5 mm, lateral nerves 8–10 on each side of the midrib, brochidodromous, inframarginal nerve 2.4–4.8 mm from the margin, tertiary nerves coarsely reticulate, raised on adaxial surface, moderately conspicuous; abaxial trichomes evenly spread, orbicular peltate scales pale red or red, 0.125–0.15 mm diam., 29–34 per 2 × 2 mm; suborbicular scales smaller and darker, 0.05–0.1 mm diam., 3–6 per 2 × 2 mm, (also appearing on the adaxial leaf surface (Fig. 13 C); abaxial stellate hairs sparse, interspersed with scales, 0.175–0.375 mm diam., 1–3 per 2 × 2 mm, each stellate hair 3–5 armed (Fig. 13 D); abaxial midrib trichomes: 1) cross-shaped scales dark red, c. 0.075 mm diam., 4–6 per 0.5 × 0.5 mm, 2) flower-shaped scales dark red, 0.075–0.1 mm diam., 2–6 per 0.5 × 0.5 mm, 3) stellate hairs 3–4 armed, dark red, 0.1–0.2 mm diam., 2–4 per 0.5 × 0.5 mm; oil glands in the midrib longitudinal, elliptic to oblong, appearing dark black in reflected light, 0.225–1.75 mm long, 2–3 per 0.5 × 0.5 mm (Fig. 13 I); oil glands of the blade only in the marginal 1/5th, obscure and usually sparse, black in transmitted and reflected light, elliptic c. 0.2 × 0.1 mm; adaxial orbicular peltate scales red or dark red, 0.075–0.1 mm diam., 7–8 per 2 × 2 mm; suborbicular scales dark red, 0.05–0.075 mm diam., 4–5 per 2 × 2 mm, adaxially otherwise glabrous. Petiole plano-convex to canaliculate (Fig. 13 B), 3–13 × 1–1.75 mm, indumentum as stem. Inflorescences axillary, fasciculate, sessile, 2 per stem, 2-flowered; bracts 2, narrowly triangular, concave, c. 1.75 × 0.5 mm, oil glands visible raised strongly on the surface, suborbicular or elliptic, appearing dark brown in reflected light, 0.075–0.175 mm diam., 3–4 per 0.25 × 0.25 mm, indumentum as stem apex, bracteoles resembling bracts, 2, c. 1.25 × 0.375 mm, indumentum as stem apex. Pedicel curving downwards, subcylindrical, 6–10 × 0.5–0.75 mm, sessile glands on the surface dark red, 2 or 3 lobed, 0.05–0.075 mm diam., 6–12 per 0.25 × 0.25 mm, oil glands visible on the surface, elliptic or oblong, dull yellow, not raised, 0.075–0.45 mm diam., c. 2 per 0.25 × 0.25 mm. Flower buds (Fig. 13 E) narrowly ovoid, drying pale brown, 4.5–5.25 × 1.9–2.25 mm, apex acute, contorted. Calyx cupular, tube 0.5 × 1.5–1.875 mm, lobes 5, broadly subtriangular, shallow, overlapping, 0.75–0.875 × 1–1.375 mm, apex acute, oil glands visible on the outer surface, orbicular or suborbicular, yellow, 0.075–0.1 mm diam., 8–10 per 0.5 × 0.5 mm, margin lined with simple hairs of 0.075–0.125 mm long. Corolla (Fig. 13 F) spreading, white, lobes 5, elliptic, 4.5–5 × 2.25–2.5 mm, glands visible on the surface, orbicular, elliptic or oblong, yellow, 0.05–0.45 mm diam., 3–6 per 0.5 × 0.5 mm; androecium yellow, stamens (Fig. 13 G) 5, erect, staminal tube present, strong pale yellow, 0.25 × 1 mm, filaments white, 0.05 × 0.5 mm, anthers introrse, dehiscing by two longitudinal slits, sagittate, yellow, 1.625 × 0.5 mm; oil glands visible on the distal connective surface, abundant, densely clustered, yellow, suborbicular or elliptic, 0.075–0.2 mm diam., 6–8 per 0.25 × 0.25 mm, connective appendage absent; ovary globose (Fig. 13 H), strong dark red, 1.125 × 1 mm, oil glands dense on the distal half; style terete, c. 3.25 mm long. Fruit not seen.

Etymology

Ardisia waka is named as a noun in apposition for the Waka National Park, Gabon from where the type and only known specimen originates.

Phenology

Flowering December.

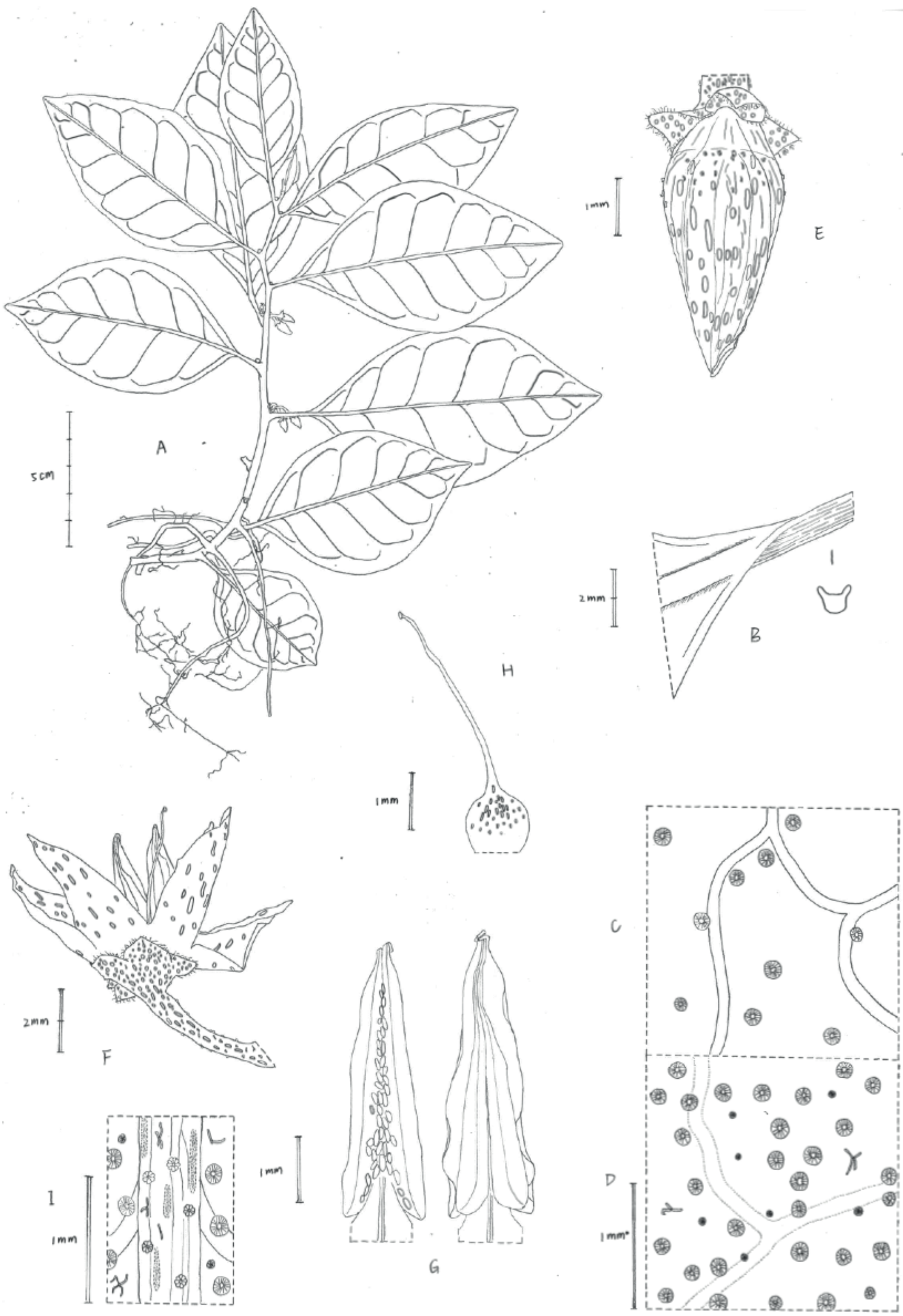

Figure 13. *Ardisia waka* P.Peng & Cheek – **A.** habit, whole plant with flower buds; **B.** base of lamina with part of petiole showing transverse section; **C.** adaxial leaf surface showing peltate scales; **D.** abaxial leaf surface showing peltate scales (larger discs), suborbicular scales (smaller discs) and stellate hairs; **E.** flower bud; F: flower, side view, inverted; **G.** stamen (dorsal face left, ventral right); **H.** ovary, style and stigma; **I.** abaxial midrib showing peltate scales (larger discs), flower-shaped scales (crenate discs), stellate hairs and oil glands (stippled oblong areas). From *A.M. Louis*, *F.J. Breteler* & *J. de Bruijn 1251*. All drawn by Peng Peng.

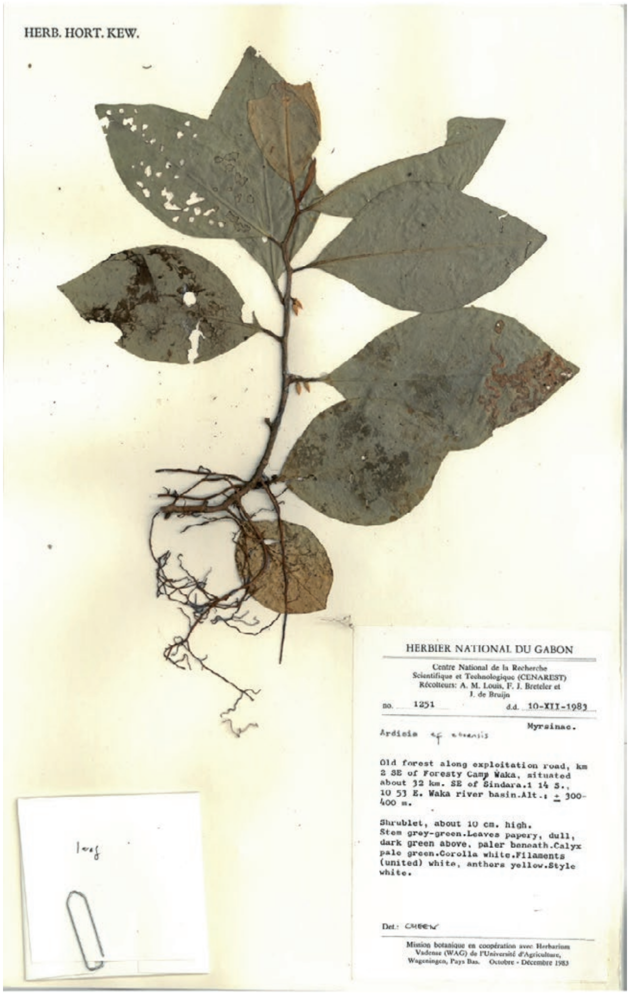

Fig. 14. Holotype of *Ardisia waka* P.Peng & Cheek.

Distribution and habitat

Ardisia waka is unique to the Waka National Park in the Chaillu Massif of Gabon in mature evergreen forest in a river basin, alt. ± 300–400 m.

Conservation status

While a single site is known (AOO 4 km^2), there appear to be no credible threats to *Ardisia waka* which is in the middle of a large National Park protected by guards (https://en.wikipedia.org/wiki/Waka_National_Park; accessed July 2025).

While some illegal hunting and logging may occur at the margins, it is not reported from the centre and in any case there is nothing to indicate that hunting would negatively affect this plant species. Therefore, for the present we assess the species as Least Concern. Should credible threats emerge the species should be reassessed as Critically Endangered.

Notes

Ardisia waka is unusual in seemingly lacking oil glands in the leaf blade except along the midrib. However, faint and inconspicuous (in both reflected and transmitted light) oil glands can be found in the marginal c. ¼ if searched for with a good microscope.

DISCUSSION

Possible bacterial nodulation in African Ardisia

During the observations for the morphological characterisation of the new species, unexpected black areas were noticed under the epidermis near the marginal teeth on the abaxial leaf-blade of some species such as *Ardisia minuta*. These black areas appeared different from the oil glands that also occur within the leaf-blade. While the oil glands are usually translucent and are distributed in a regular pattern throughout the leaf blade, the black areas were opaque and restricted to marginal areas. Further, the black areas occur along the veinlets that lead to the apex of the teeth where they can terminate in pores. The same observations were made in other herbaceous species e.g. *A. chaillu* (Fig. 1E), A. *massaha* (Fig 5D) and *A. ngounie* (Fig. 9E). In the literature review conducted at the start of the project, references were found to bacterial colonisation in one group of Asian *Ardisia* species, the *Ardisia crenata* group, yet it is stated that such colonisation in *Ardisia* is only known within that species group and not elsewhere in the genus (Yang & Hu 2018). Investigation of the literature showed that the leaves of those Asian species are colonised when in bud stage at the stem apex from an exudate, the *Paraburkholderia* bacteria entering through the developing leaf through the marginal teeth pores (Lersten and Horner 1976; Lemaire et al. 2011). The bacterial colonisation in the *Ardisia crenata* group results in regular patterns. The markings observed in this research project for the African herbaceous species are less regular but still distinct. To date confirmation by direct observation of bacterial rods using SEM has not been possible, also, this was not the focal point of the project which is alpha taxonomic elucidation of the species of *Ardisia*. It is intended to investigate the bacterial colonisation in greater depth in the future. Bacteria are also known to colonise African Rubiaceae (Lersten and Horner 1976). Four genera of African Rubiacaeae are now known to be colonised (Cheek and Onana 2024). Studies have shown that the same lineage of bacteria that colonise Asian *Ardisia* also colonise African Rubiaceae, the Asian *Ardisia* bacterial taxa being basal in the lineage, while the African Rubiaceae endosymbiont taxa are terminal (Lemaire et al. 2011; Pinto-Carbó et al. 2018). If bacterial colonisation is confirmed in African *Ardisia* we postulate that they are likely sister to African Rubiaceae taxa rather than the Asia *Ardisia* taxa because African herbaceous *Ardisia* are sympatric with African Rubiaceae with bacterial nodules which are much more frequent and species diverse in the range of the herbaceous *Ardisia* (Cameroon and Gabon) than are the *Ardisia* species (Cheek pers. obs. 1991 onwards). Lemaire et al. (2011) have shown that horizontal transfer of bacteria from the environment to plants has occurred multiple times and reject long co-speciation of plants and endosymbiotic bacteria.

Geographic and morphological species groupings

Large peltate leaf-scales (c. 0.1 mm diam.) are only found in the Gabonese species, excepting *A. hansii* which occurs both in Gabon and in the South Region of Cameroon. Of the Gabonese species, only *A. massaha* (northeastern Gabon) shares the absence of these large scales with the three Cameroon endemic species. While in Cameroon two of the species occur at sea-level in coastal forest, the other Cameroonian endemic and all of the Gabonese species are associated with the lower slopes of inland submontane areas, several species (*A. chaillu*, *A. ebo*, *A. hansii*) reaching 800 m alt. (which is often taken as the lower boundary of submontane or cloud forest) and *A. massaha* reaches c. 950 m alt. Most of the species are not sympatric. However, three species occur in different parts of the Chaillu Massif which appears the centre of diversity for the group, followed by Belinga (two species). The three Chaillu species all share sessile globose glands on the pedicels. Also in fruit (unknown in *A. waka*), the pedicels are erect.

CONCLUSIONS

It is important to detect, delimit and formally name species such as those in this paper as new to science, since until they are scientifically recognised, they are essentially invisible, and only when they have a scientific name can their inclusion on the IUCN Red List be facilitated (Cheek et al. 2020). Most (77%) species named as new to science today are already threatened with extinction (Brown *et al.* 2023). All but one of the six new species in this paper are provisionally assessed as threatened. Many new species to science have evaded detection until today, because they are in genera that are long overdue in terms of a full taxonomic revision, as is the case in *Ardisia* (not revised for 45 years), or because they have minute ranges which have remained unsurveyed until relatively recently, as has also been the case with herbaceous *Ardisia* especially in Gabon.

If further global extinction of plant species is to be avoided, effective conservation prioritization is crucial, backed up by investment in protection of habitat, ideally through reinforcement and support for local communities who often effectively manage the areas concerned. Important Plant Areas (IPAs) programmes, often known in the tropics as TIPAs (Darbyshire et al. 2017; Murphy et al. 2023) offer the means to prioritize areas for conservation based on the inclusion of highly threatened plant species, among other criteria. Such measures are vital if further species extinctions are to be avoided of rare, highly threatened species as is feared has occurred already with *Ardisia sadebeckiana* and *A. schlechteri* in Cameroon.

Limitations and further work

This study is mainly based on specimens from the herbarium of the Royal Botanic Gardens, Kew (K) and those loaned from the National Herbarium of the Netherlands, Wageningen (WAG) at Naturalis, and the Meise Botanical Garden (BR), supplemented by some observations during a short visit to the Paris Herbarium (P) and the Natural History Museum (BM). However, we were not able to access specimens at the two principal herbaria for Cameroon (YA) and Gabon (LBV), nor that for the Republic of Congo (IEC) due to both timing (most of this study was conducted in the covid years) and lack of funds and permits. It is likely that additional records of species of this group, including further new species, will result from these countries when this deficiency can be addressed. Important specimens at Herbarium Hamburgense (HBG) were available only as digital images, so studies of the physical specimens are advisable to enhance this study.

In this study much progress has been made resolving species limits in the herbaceous, creeping African *Ardisia*. A further and more ambitious project is to repeat this study for the woody species of African *Ardisia*. In addition, molecular phylogenetic work would be highly valuable to resolve the evolutionary relationships of the different species of African *Ardisia* groups identified in this study.

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REFERENCES

Anon. 1905. Scientific Notes and Views, Science, New Series. 21(536): 556 https://www.jstor.org/stable/1630357?seq=

Beentje H. 2016. The Kew Plant Glossary: An Illustrated Dictionary of Plant Terms. Royal Botanic Gardens, Kew, London.

Cable S, Cheek M. 1998. The Plants of Mt Cameroon, a Conservation Checklist. Royal Botanic Gardens, Kew.

Capuron R. 1963. Le genre *Ardisia* Swartz (Myrsinacées) a Madagascar. Adansonia ser. 2(3): 384

Chapman J, Chapman H. 2001. The Forests of Taraba and Adamawa States, Nigeria an Ecological Account and Plant Species Checklist. University of Canterbury: Christchurch, New Zealand. Pp. 221.

Cheek M, Cable S. 1997. Plant Inventory for conservation management: the Kew-Earthwatch programme in Western Cameroon, 1993–96: 29–38. In Doolan S. (Ed.) African Rainforests and the Conservation of Biodiversity. Earthwatch Europe, Oxford.

Cheek M, Cable S. 2000a. *Ardisia etindensis*. The IUCN Red List of Threatened Species 2000:e.T39527A10245428. https://doi.org/10.2305/IUCN.UK.2000.RLTS.T39527A10245428.en. Accessed on 11 July 2025.

Cheek M, Cable S. 2000b. *Ardisia schlechteri*. The IUCN Red List of Threatened Species 2000:e.T39529A10245538. https://doi.org/10.2305/IUCN.UK.2000.RLTS.T39529A10245538.en. Accessed on 24 April 2025.

Cheek M, Onana JM. 2024. *Keetia nodulosa* sp. nov. (Rubiaceae-Vanguerieae) of West-Central Africa: bacterial leaf nodulation discovered in a fourth genus and tribe of Rubiaceae. Webbia. 79(1): 31–46. https://doi.org/10.36253/jopt-15946

Cheek M, Williams S. 1999. A Review of African Saprophytic Flowering Plants: 39–49. In: Timberlake J, Kativu S. (Eds.) African Plants. Biodiversity, Taxonomy & Uses. 15th AETFAT Congress, Harare, Zimbabwe.

Cheek M, Xanthos M. 2012. *Ardisia ebo* sp. nov. (Myrsinaceae), a creeping forest subshrub of Cameroon and Gabon. Kew Bulletin. 67(2): 281. https://doi.org/10.1007/s12225-012-9362-8

Cheek M, Cable S, Hepper FN, Ndam N, Watts J. 1996. Mapping plant biodiversity on Mt. Cameroon: 110–120. In: van der Maesen, van der Burgt, van Medenbach de Rooy (Eds.), The Biodiversity of African Plants (Proceedings XIV AETFAT Congress. Kluwer.

Cheek M, Etuge M, Williams S. 2019. *Afrothismia kupensis* sp. nov. (Thismiaceae), Critically Endangered, with observations on its pollination and notes on the endemics of Mt Kupe, Cameroon. Blumea. 64: 158–164. https://doi.org/10.3767/blumea.2019.64.02.06

Cheek M, Feika A, Lebbie A, Goyder D, Tchiengue B, Sene O, Tchouto P, van der Burgt X. 2017. A synoptic revision of *Inversodicraea* (Podostemaceae). Blumea. 62: 125–156. https://doi.org/10.3767/blumea.2017.62.02.07

Cheek M, Harvey YB, Onana J-M. 2010. The Plants of Dom. Bamenda Highlands, Cameroon: A Conservation Checklist. Royal Botanic Gardens, Kew.

Cheek M, Harvey YB, Onana J-M. 2011. The Plants of Mefou Proposed National Park. Yaoundé, Cameroon: A Conservation Checklist. Royal Botanic Gardens, Kew.

Cheek M, Nic Lughadha E, Kirk P, Lindon H, Carretero J, Looney B, Douglas B, Haelewaters D, Gaya E, Llewellyn T, Ainsworth M, Gafforov Y, Hyde K, Crous P, Hughes M, Walker BE, Forzza RC, Wong KM, Niskanen T. 2020. New scientific discoveries: plants and fungi. Plants, People Planet. 2: 371–388. https://doi.org/10.1002/ppp3.10148

Cheek M, Onana J-M, Pollard BJ. 2000. The Plants of Mount Oku and the Ijim Ridge, Cameroon, a Conservation Checklist. Royal Botanic Gardens, Kew.

Cheek M, Pollard BJ, Darbyshire I, Onana JM, Wild C. 2004. The Plants of Kupe, Mwanenguba and the Bakossi Mts, Cameroon. A Conservation Checklist. Royal Botanic Gardens, Kew.

Cheek M, Prenner G, Tchiengué B, Faden RB. 2018. Notes on the endemic plant species of the Ebo Forest, Cameroon, and the new, Critically Endangered, *Palisota ebo* (Commelinaceae). Plant Ecology & Evolution. 151(3): 434–441. https://doi.org/10.5091/plecevo.2018.1503

Cheek M, Sidwell K, Sunderland T, Faruk A. 1992. A Botanical Inventory of the Mabeta-Moliwe Forest. Royal Botanic Gardens, Kew; report to Govt. Cameroon from O.D.A.

Cheek M, Soto Gomez M, Graham SW, Rudall PJ. 2024. Afrothismiaceae (Dioscoreales), a new fully mycoheterotrophic family endemic to tropical Africa. Kew Bulletin. 1–19. https://doi.org/10.1007/s12225-023-10124-w

Cheek M, Tsukaya H, Rudall PJ, Suetsugu K. 2018. Taxonomic monograph of *Oxygyne* (Thismiaceae), rare achlorophyllous mycoheterotrophs with strongly disjunct distribution. PeerJ. 6: e4828. https://doi.org/10.7717/peerj.4828

Darbyshire I, Anderson S, Asatryan A, Byfield A, Cheek M, Clubbe C, Ghrabi Z, Harris T, Heatubun CD, Kalema J, Magassouba S, McCarthy B, Milliken W, Montmollin B de, Nic Lughadha E, Onana JM, Saıdou D, Sarbu A, Shrestha K, Radford EA. 2017. Important Plant Areas: revised selection criteria for a global approach to plant conservation. Biodiversity Conservation. 26: 1767–1800. https://doi.org/10.1007/s10531-017-1336-6

Davies NMJ, Drinkell C, Utteridge TMA. 2023. The Herbarium Handbook. Kew Publishing

de Wit HCD. 1958. Revision of *Afrardisia* Mez (Myrsinaceae). Blumea. 4 (supplement): 242–262.

Dzoyem JP, Ndontsa BL, Santosh KG, Inshad A, Khan ASK, Vishwakarma RA, Tane P. 2014. Antiproliferative and antimicrobial activities of alkylbenzoquinone derivatives from *Ardisia kivuensis*. Pharmaceutical Biology. 52(3): 392–397, https://doi.org/10.3109/13880209.2013.837076

GBIF. continuously updated. Global Biodiversity Information Facility [online]. Available from https://www.gbif.org/occurrence/map?taxon_key=3169458&occurrence_status=present. Aaccessed 9 Feb. 2021.

Ghogue J.-P. 2010. *Ledermanniella batangensis*. The IUCN Red List of Threatened Species 2010: e.T185525A8428951. https://doi.org/10.2305/IUCN.UK.2010-3.RLTS.T185525A8428951.en. Accessed on 14 July 2025.

Gilg E. 1902. Myrsinaceae africanae. Botanische Jahrbücher fur Systematik, Pflanzengeschichte und Pflanzengeographie. 30: 95–101. https://www.biodiversitylibrary.org/page/211309#page/100/mode/1up

Gilg E, Schellenberg G. 1913. Myrsinaceae africanae. II.Botanische Jahrbücher fur Systematik, Pflanzengeschichte und Pflanzengeographie. 48: 512–525 https://www.biodiversitylibrary.org/item/136883#page/552/mode/1up

Good RD. 1927. Myrsinaceae. Journal of Botany, British and foreign. 65(supplement): 69.

Gosline G, Cheek M, Onana JM, Ngansop Tchatchouang E, van der Burgt XM, MacKinnon L, Dagallier LMJ. 2022. *Uvariopsis dicaprio* (Annonaceae) a new tree species with notes on its pollination biology, and the Critically Endangered narrowly endemic plant species of the Ebo Forest, Cameroon. PeerJ. Jan 6; 9:e12614. https://doi.org/10.7717/peerj.12614

Halliday P. 1984 Myrsinaceae. In: Polhill RM (Ed.) ,Flora of Tropical East Africa: 16–19. Balkema, Rotterdam.

Harvey YB, Pollard BJ, Darbyshire I, Onana J-M, Cheek M. 2004. The Plants of Bali Ngemba Forest Reserve. Cameroon: A Conservation Checklist. Royal Botanic Gardens, Kew.

Harvey YB, Tchiengue B, Cheek M. 2010. The Plants of the Lebialem Highlands, a Conservation Checklist. Royal Botanic Gardens, Kew.

Hepper FN. 1963. Flora of West Tropical Africa 2: 31. Crown Agents, London.

IPNI. continuously updated. The International Plant Names Index. http://ipni.org/ (accessed: 07/2023).

IUCN. 2012. IUCN Red List Categories and Criteria: Version 3.1. Second edition.–Gland, Switzerland and Cambridge, UK: IUCN. Available from: http://www.iucnredlist.org/. Accessed on April 2025.

Julius A, Utteridge TMA. 2012. Revision of *Ardisia* subgenus *Bladhia* in Peninsular Malaysia; studies in Malaysian Myrsinaceae I. Kew Bulletin. 67(3): 379–388. https://doi.org/10.1007/s12225-012-9374-4

Julius A, Utteridge TMA. 2021. *Ardisia recurvisepala* (Primulaceae-Myrsinoideae), a new species from Peninsular Malaysia. Phytotaxa. 480(1): 79-84. https://doi.org/10.11646/phytotaxa.480.1.7

Julius A, Utteridge TMA. 2022. *Ardisia whitmorei* (Primulaceae-Myrsinoideae), a new species from Peninsular Malaysia. PhytoKeys. 204: 35–41. https://doi.org/10.3897/phytokeys.204.86647

Julius A, Kajita T, Utteridge TMA. 2017. *Ardisia gasingoides* (Primulaceae-Myrsinoideae), a new species from southern Peninsular Malaysia. Phytotaxa. 291(4): 281–286. https://doi.org/10.11646/phytotaxa.291.4.5

Julius A, Gutiérrez-Ortega JS, Sabran S, Tagane S, Naiki A, Darnaedi, D, Aung M, Dang S, Nguyen N, Binh H, Watano Y. 2021. Phylogenetic relationship of tropical Asian Ardisia and relatives (Primulaceae) shows non-monophyly of recognized genera and subgenera. Shokubutsu Kenkyu Zasshi. 93: 149–165.

Julius A, Siti-Munirah MY, Utteridge TMA. 2023. *Ardisia recurvipetala* (Primulaceae-Myrsinoideae), a new species from northern Peninsular Malaysia. PhytoKeys. 232: 89–98. https://doi.org/10.3897/phytokeys.232.103649

Kitajima K, Fox AM, Sato T, Nagamatsu D. 2006. Cultivar selection prior to introduction may increase invasiveness: evidence from *Ardisia crenata*. Biological Invasions. 8:1471–1482. https://doi.org/10.1007/s10530-005-5839-9

Larsen K, Hu CM. 1995. Reduction of *Tetrardisia* to *Ardisia*. Nordic Journal of Botany. 15: 161–162. https://doi.org/10.1111/j.1756-1051.1995.tb00134.x

Larson DA, Chanderbali AS, Maurin O, Gonçalves DJ, Dick CW, Soltis DE, Utteridge TM. 2023. The phylogeny and global biogeography of Primulaceae based on high-throughput DNA sequence data. Molecular Phylogenetics and Evolution. 182: 107702. https://doi.org/10.1016/j.ympev.2023.107702

Lemaire B, Vandamme P, Merckx V, Smets E, Dessein S. 2011. Bacterial leaf symbiosis in angiosperms: host specificity without co-speciation. PLoS One. 6(9): e24430. https://doi.org/10.1371/journal.pone.0024430

Lersten NR, Horner HT. 1976. Bacterial leaf nodule symbiosis in angiosperms with emphasis on Rubiaceae and Myrsinaceae. Botanical Review. 42: 145–214 https://doi.org/10.1007/BF02860721

Liu B, Liu R, Liu Q, Ashby Jr CR, Zhang, H, Chen ZS. 2022. The ethnomedicinal and functional uses, phytochemical and pharmacology of compounds from *Ardisia* species: an updated review. Medicinal Research Reviews. 42(5): 1888–1929. https://doi.org/10.1002/med.21894

Lockwood H, Tchatchouang EN. 2025. *Begonia ebo* sp. nov. (Sect. Filicibegonia-Begoniaceae), endangered in Ebo, a highly threatened forest in Littoral Region, Cameroon. Webbia. 80(1): 77–87. https://doi.org/10.36253/jopt-17739

Lovell R, Cheek M. 2020. *Ardisia ebo*. The IUCN Red List of Threatened Species 2020: e.T172490315A172490333. https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T172490315A172490333.en. Accessed on 13 April 2025.

Magtoto LM, Tamayo MN, Udasco LC, Bustamante RAA. 2021. *Ardisia kalimbahin* (Primulaceae, Myrsinoideae), a new species from the Philippines. Phytotaxa. 525: 4 doi:10.11646/phytotaxa.525.4.4

Mao SZ, Hu CM. 2013. *Ardisia rubricaulis* sp. nov. (Primulaceae) from Guangxi, China. Phytotaxa. 138(1): 39–42. https://doi.org/10.11646/phytotaxa.138.1.5

Maisels FM, Cheek M, Wild C. 2000. Rare plants on Mt Oku summit, Cameroon. Oryx. 34: 136–140. https://doi.org/10.1017/s0030605300031057

Mez, C. 1902. Myrsinaceae. In: Engler A. (Ed.), Das Pflanzenreich, Heft 9 (IV. Fam. 236). Verlag von Wilhelm Engelmann, Leipzig, 437 pp.

Murphy B, Onana JM, van der Burgt XM, Tchatchouang Ngansop E, Williams J, Tchiengué B, Cheek M. 2023. Important Plant Areas of Cameroon. Royal Botanic Gardens, Kew.

Nuraliev MS, Kuznetsov AN, Kuznetsova SP, & Hu CM. 2021. *Ardisia patentiradiosa* (Primulaceae), a new species from southern Vietnam. Phytotaxa. 522(1): https://doi.org/10.11646/phytotaxa.522.1.7

Oliver D. 1877. Flora of Tropical Africa 3: 495. L. Reeve and Company, London.

Onana J-M. 2011. The Vascular Plants of Cameroon. A Taxonomic Checklist with IUCN Assessments. Flore Du Cameroun 39. Ministry of Scientific Research and Innovation, Yaoundé, Cameroon.

Onana JM, Cheek M. 2011. Red Data Book of the Flowering Plants of Cameroon, IUCN Global Assessments. Royal Botanic Gardens, Kew.

Perrier de la Bâthie H. 1952. Pharmacopée malgache. Mémoires de l'Institut Scientifique de Madagascar. Série B. Biologie Végetale 4:207.

POWO continuously updated. The Plants of the World online [online]. Available from http://www.plantsoftheworldonline.org/. Accessed on 29 Jan. 2025.

Pinto-Carbó M, Gademann K, Eberl L, Carlier A. 2018. Leaf nodule symbiosis: function and transmission of obligate bacterial endophytes. Current opinion in plant biology. 44: 23–31. https://doi.org/10.1016/j.pbi.2018.01.001

Quan D-L, Tan YH. 2024. *Ardisia chimingiana* (Primulaceae), a New Species from Yunnan, China. Annales Botanici Fennici. 61(1): 7–15 https://doi.org/10.5735/085.061.0102

Simpson, W. (continuously updated). *Ardisia crenata*, coral berry in: https://www.fdacs.gov/Agriculture-Industry/Pests-and-Diseases/Plant-Pests-and-Diseases/Noxious-Weeds/Ardisia-crenata-Coral-Ardisia . Accessed July 2025.

Sosef MSM, Wieringa JJ, Jongkind CCH, Achoundong G, Azizet Issembé Y, Bedigian D, Van Den Berg RG, Breteler FJ, Cheek M, Degreef J. 2006. Check-list des plantes vasculaires du Gabon. Scripta Botanica Belgica 35: 1-435. National Botanic Garden of Belgium.

Ståhl B, Anderberg AA. 2004. Myrsinaceae. In: Kubitzki K. (Ed.), The Families and Genera of Vascular Plants 6: 266–281. Springer, Berlin.

Stone RD, Tchiengué B, Cheek M. 2024. The endemic plant species of Ebo Forest, Littoral Region, Cameroon with a new Critically Endangered cloud forest shrub, *Memecylon ebo* (Melastomataceae-Olisbeoideae). Kew Bulletin. 79: 867–879. https://doi.org/10.1007/s12225-024-10223-2

Swartz O. 1788. Nova Genera & Species Plantarum seu Prodromus descriptionum Vegetabilium, maximam partem incognitorum quae sub itinere in Indiam Occidentalem annis 1783–87. Acad. M. Swederi, Stockholm. https://doi.org/10.5962/bhl.title.4400

Taton S. 1979. Contribution à l'étude du genre *Ardisia* Sw. (Myrsinaceae) en Afrique tropicale. Bulletin du Jardin Botanique National de Belgique. 49(1–2): 91–114. https://doi.org/10.2307/3667819

Taton S. 1980. Myrsinaceae. Flore d'Afrique Centrale: 12–29, National Botanic Garden, Meise.

Taton S, Lejoly J. 1980. Une espèce nouvelle d' *Ardisia* (Myrsinaceae) du Zaïre. Bulletin du Jardin Botanique National de Belgique. 50(1–2): 463. https://doi.org/10.2307/3667783

Thiers B. 2025. (continuously updated). Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. [continuously updated].–Available from: http://sweetgum.nybg.org/ih/. Accessed on Feb. 2023.

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber W-H, Li D-Z, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF. (Eds.) 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile. 159. Glashütten: Koeltz Botanical Books.

Tzinieris S. 2014. Bidding for untapped Gabon iron ore reserve, world's largest, could spark mining sector. War Studies. https://kclpure.kcl.ac.uk/portal/en/publications/bidding-for-untapped-gabon-iron-ore-reserve-worlds-largest-could-. Accessed on April 2025.

Wildeman ED. 1925. Plantae Bequaertianae Etudes sur les Récoltes Botaniques du Dr. J. Bequaert Chargé de Missions au Congo Belge (1913–1915). 3: 216, Lechevalier, Paris.

Yang CJ, Hu JM. 2018. Bacterial Leaf Nodule Symbiosis in Flowering Plants, Symbiosis. IntechOpen. https://www.intechopen.com/chapters/58848

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Novelties in *Bakerella* (Loranthaceae) from Madagascar

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Abstract. Recently it became clear that at least some of the varieties and subspecies that are currently recognised in *Bakerella* Tiegh. (Loranthaceae) from Madagascar are better placed as species. In several cases these taxa were originally already described as species but not yet in *Bakerella*, so new combinations are needed. The first four new combinations are published here.

Keywords: *Bakerella*, endemic, Loranthaceae, Madagascar, mistletoe, taxonomy.

INTRODUCTION

On Madagascar there are currently only two genera of Loranthaceae recognized, *Bakerella* Tiegh. and *Socratina* Balle, both of which are endemic to the island (Callmander 2014). *Bakerella* can easily be separated from *Socratina* by its glabrous branches and leaves and by its anthers that are longer than their filaments. Balle was the first to use *Bakerella* in its current circumscription (Balle 1964a & b); in the "Flore de Madagascar et des Comores" the genus includes 16 species (Balle 1964b). The key to the species in the "Flore" is not easy to use, and consequently many specimens collected after 1964 remained unidentified or are misidentified. With the emergence of digital cameras, many photos of flowering plants have been made on Madagascar. For *Bakerella* that is important news, when you know the often characteristic colour of the corolla it is much easier to recognize and separate most species. With these photos at hand a new attempt to identify the herbarium specimens of *Bakerella* was made as a start for a new revision of the genus. During this identification work it became clear that some of the varieties and subspecies that were used by Balle in 1964 are better recognised as species. In several cases these taxa were originally described as species but not yet in *Bakerella*, so new combinations are needed. A first selection of these nomenclatural novelties is published here. In the coming year more new combinations, and probably some new species, will be published.

MATERIAL AND METHODS

This publication is the result of a morphological study of the herbarium material kept at BR, K and WAG (Thiers, continuously updated). Online databases used to study scans of more herbarium material and photos of living plants were those facilitated by the Muséum national d'Histoire naturelle in Paris [https://science.mnhn.fr], Tropicos from Missouri Botanical Garden [http://www.tropicos.org], iNaturalist [https://www.inaturalist.org/observations], the African Plant Database [https://africanplantdatabase.ch/], Sweden's Virtual Herbarium [http://herbarium.emg.umu.se] and the JSTOR Global Plants website [https://plants.jstor.org/].

All cited specimens have been seen as a herbarium sheet, scan of a sheet or field photo. A sheet is seen in person when "!" is added to a cited herbarium specimen, in all other cases a detailed scan of a sheet from that herbarium is seen, or a field photo made for that institute.

Figure 1. Flowers of *Bakerella alata* (Balle) Jongkind. (by Ulf Swenson after Swenson 1809).

Figure 2. Flowers of *Bakerella alata* (Balle) Jongkind. (by Christopher Davidson after Rogers 860).

TAXONOMIC TREATMENT

Bakerella alata (Balle) Jongkind, **comb. nov**. (Figures 1-3).

Bas.: *Bakerella poissonii* (Lecomte) Balle subsp. *poissonii* var. *alata* Balle, Adansonia, n.s., 4: 116. 1964a.

Type: Madagascar, Morondava, fl., *Greve 1* [holotype (P barcode P05097155 scan); isotypes K! (barcode K004552875, P barcode P05097154 scan)].

Short description

Leaf blade elliptic to narrowly obovate, 1.8-5 × 0.5-2 cm, with 1-5 just visible parallel veins ascending from base almost to the apex, apex rounded, petiole 3-6 mm. Inflorescences axillary, fascicles of a few or several flowers, pedicel c. 2 mm long. Calyx c. 1 mm long, membranous, collar-shaped, easily falling apart. Corolla 2.5-3.7 cm long, clearly narrowly winged (most easily visible in the upper part of the mature bud), yellow to orange-red, base inflated, lobes slightly reflexed at anthesis. Anthers 4.5-5 mm long.

Comments

Bakerella alata and *B. parvibracteata* were included by Balle (1964a & b) in *B. poissonii* because they all share the same kind of membranous, collar-shaped, calyx, that easily falls apart. The three species have different distributions without overlap (Fig. 3). *B. poissonii* (s.s.) has a pinkish corolla tube, often a bit lilac, while the other two have a bright yellow and/to orange-red corolla. Balle had seen only two specimens of *B. alata* (*B. poissonii* var. *alata*) and from one of those, Humbert 28787, she was not sure it was really this taxon. Today we have more specimens and we also can see the striking colour of the corolla on several photos.

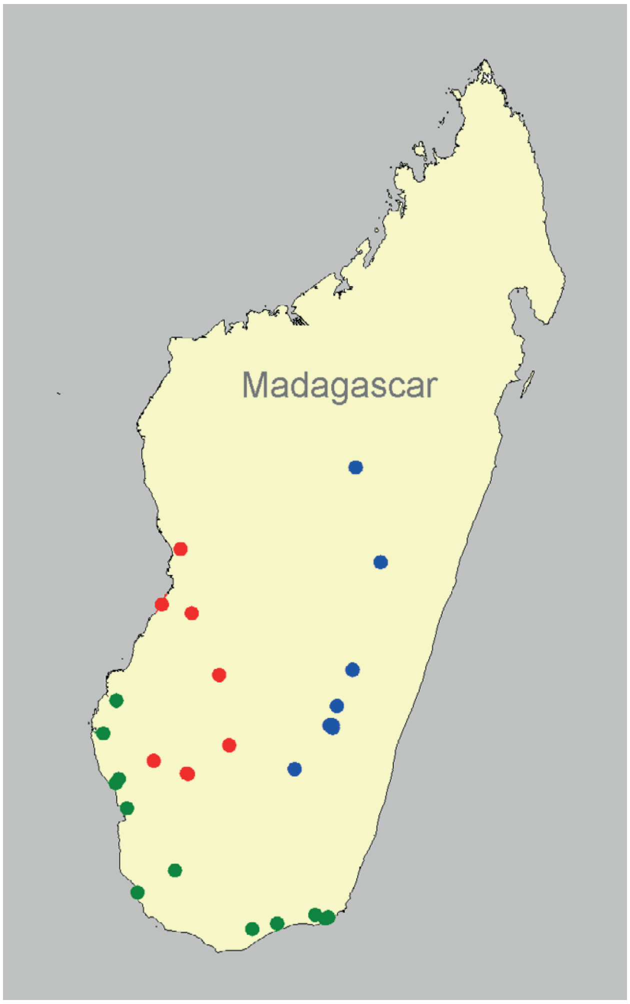

Figure 3. Distribution map. *B. alata* (Balle) Jongkind (red dots). *B. parvibracteata* (Lecomte) Jongkind (blue dots). *B. poissonii* (Lecomte) Balle (green dots).

Other specimens studied

MADAGASCAR. c 36 km NE of Belo sur Tsiribihina, c. 40 m, 31 Mar 1990, fl., *Du Puy 815* (BR!, K!, P scan); W de Ranohira, Hte vallée de la Malio, 1955, fl., *Humbert 28787* (P scan); Mahabo, Dabara, 1 km S of the bridge, 98 m, 18 Jun 2016, fl., *Onjalalaina 1153* (P scan); Beronono-Makay, 395 m, 14 Jan 2010, fl., *Rakotovao 5083* (P scan); Forêt d'Analavelona, Campement Antanimena, 1093 m, 19 Apr 2012, fl., *Razanatsima 1043* (P scan); Ambakitany Forest, N of National Route #7, 800-830 m, 13 Jan 2006, fl., *Rogers 860* (MO photos, P scan); Zombitsy-Vohibasia National Park, eastern forest edge, north of the road, 800 m, 25 Jan 2018, fl., *Swenson 1809* (P scan, S photos).

Bakerella amplifolia (Balle) Jongkind, **comb. nov**. (Figures 4-6).

Bas.: *Bakerella clavata* (Desr.) Balle subsp. *clavata* var. *amplifolia* Balle, Adansonia, n. s., 4: 110 1964a.

(–) *Loranthus amplifolius* Lecomte, Notul. Syst. (Paris) 4: 39. 1923, *nom. illegit*. [not *Loranthus amplifolius* Merr., Philipp. J. Sci., C 13: 277 (1918)].

Type: Madagascar, Tsaratanana, 2000 m, Oct 1912, fl., *Perrier de la Bâthie 10701* [holotype P (barcode P00752520), isotype P (barcode P00752519, scans)].

Short description

Leaf blade 7-18 × 5.5-8.5 cm, coriaceous, most leaves gradually narrowing to an acute apex, venation pinnate, secondary veins ascending from their base, petiole 0–1.5 cm long. Inflorescence one, or a few together, in the axil of a leaf, almost sessile, single flowered or in an umbel with 2-4 flowers. Calyx 1.5-2 mm long. Corolla 4-4.5 cm long, slightly carnose, never inflated at base, mature bud reddish at the base changing to pale dull yellowish higher up, later completely pink-red, lobes 7-8 mm long, slightly reflexed. Anthers c. 3 mm long.

Figure 4. Inflorescence of *Bakerella amplifolia* (Balle) Jongkind. (by Louis Nusbaumer after Nusbaumer 5111 (G)).

Figure 5. Flowers of *Bakerella amplifolia* (Balle) Jongkind. (by Louis Nusbaumer after Nusbaumer 5111 (G)).

Figure 6. New leaves of *Bakerella amplifolia* (Balle) Jongkind. (by Louis Nusbaumer after Nusbaumer 5111 (G)).

Comments

All other taxa included by Balle in *B. clavata* have in common that every plant has the majority of its flowers in two flowered umbels. *Bakerella amplifolia* (as *B. clavata* var. *amplifolia*) is an exception with 1 - 4 flowers in one inflorescence. Balle did not explain why she included this former species in *B. clavata*. With its slightly carnose corolla, and umbels with more than 2 flowers, *B. amplifolia* shares characters with *B. grisea* (Scott Elliot) Balle. *B. amplifolia* differs from *B. grisea* by its reddish and pale dull yellowish corolla, versus a corolla that is mainly bright yellow and orange. The corolla of *B. grisea* is also more carnose.

Bakerella amplifolia is only known from forests in the north of Madagascar between 880-2000 m elevation.

Other specimens studied

MADAGASCAR. Tsaratanana Massif, southern slopes, Ampanopia, 882 m, 30 Oct 2000, fl., *Antilahimena 629* (K!, P scan); Forêt de Sorata, 1410 m, 8 Feb 2022, fr., *Havinga & Iharivolana 255* (BR!, G photo); Massif du Tsaratanana et Haute Vallée de Sambirano, 1400-1800 m, Nov-Dec 1937, fl., *Humbert 18228* (P scan); idem, c. 2000 m, *Humbert 18618* (P scan); Forêt de Sorata, 1410 m, 12 Dec 2021, fl., *Nusbaumer et al. 5111* (BR!, G photos); Tsaratanana, c. 2000 m, Dec 1922, fr., *Perrier de la Bâthie 15573* (P scan).

Bakerella marojejensis (Balle) Jongkind, **comb. nov**. (Figures 7, 8).

Bas.: *Bakerella viguieri* (Lecomte) Balle var. *marojejensis* Balle, Adansonia, n.s., 4: 117. 1964a.

Type: Madagascar, Pentes orientales de Massif de Marojejy, à l' ouest de la rivière Manantenina, 1400 m, 15-25 Dec 1948, fl., *Humbert 22499* [holotype P (barcode P05066487, scan)].

Short description

Leaf blades very variable (4-18 × 1.5-11 cm), especially between individual plants, apex always acute to acuminate, secondary venation pinnate, usually spreading (not strongly ascending) and midrib raised above and below. Inflorescences usually with a single flower on a short peduncle, with one or more in a leaf axil, often with many together on the old wood. Corolla strongly angular in cross section to slightly winged especially near the top, in bud lower part pinkish, the upper part greenish-yellow, in open flower often completely red and usually clearly inflated at the base and around the middle.

Comments

Bakerella marojejensis is only found in the north of Madagascar in forests at c. 700 – 1500 m elevation. According to Balle, *B. marojejensis* (*B. viguieri* var. *maro-*

Figure 7. *Bakerella marojejensis* (Balle) Jongkind. Flowers and part of leaf showing the raised midrib. (by Charles Rakotovao (Tropicos) after Rakotovao 2683).

Figure 8. *Bakerella marojejensis* (Balle) Jongkind. Flowering on the leafless stem or branch. (by Éric Mathieu (Marojejy, Oct 2007)).

jejensis) occurs in the "montagnes du Centre-Nord" and "le Centre moyen" of Madagascar (Balle 1964a) but she cited only one specimen from the south, Humbert 3608 (Haute vallée de la Rienana, bassin du Matitanana), and that one does not belong to this species.

Balle separated *Bakerella vigueiri* (Lecomte) Balle, with its two varieties viguieri and marojejensis, from related species by its uniflorous umbels or, in other words, with every single flower on its own (short) peduncle separated by an articulation. Apart from this shared character, the two varieties are conspicuously different in leaves and flowers. The corolla of *B. marojejensis* is strongly angular to narrowly winged from base to top, that of *B. viguieri* is almost circular in cross-section. The leaves of *B. marojejensis* have an acute or sometimes acuminate apex, a spreading pinnate venation and a raised midrib, whilst the leaves of *B. viguieri* have a rounded apex, a less conspicuous pinnate venation with ascending secondary veins and a flat or channelled midrib.

Selection of specimens studied

MADAGASCAR. Ambatoledama, Jun 2003, fl., *Antilahimena 2034* (P scan); Anjanaharibe-Sud Special Reserve, 1520 m, 19/20 May 1999, fl., *Birkinshaw 594* (P scan); Montagne de Ambosotoratra, 3 Jan 1949, fl., *Cours 3274* (P scan); Marojejy RNI no. 12, path from Mandena to the summit of Marojejy, 1000-1300 m, 29 Sep 1994, fl., *Lewis 1145* (P scan, WAG!); along trail from Andranomadio to Tsaratanana peak, 2500 m, 18 Oct 2001, fl., *Lowry 5404* (K!); Parc National de Marojejy, 11 km NW du village Manantenina, 14°26.2'S 49°44.5'E, 1200 m, 31 Oct 1996, fl., *Messmer 297* (P scan); along the trail to the summit of Marojejy Est, 700-850 m, 10 Feb 1989, fl., *Miller 3901* (K!, MO photo, WAG!); 3,32 km E du sommet de Marojejy, 16 Feb 2014, fl., *Onjalalaina 279* (K!); à 1,5 Km Est du village de Marovato, 710 m, 16 Feb 2006, fl., *Rakotovao 2683* (MO photo, P scan); à 10 km au Nord-Ouest d'Andranopositra, 1159 m, 18 Nov 2006, fl., *Rakotovao 3431* (P scan); c. 13 Km à l'Ouest du village d'Andranopositra, 1429 m, 7 Nov 2006, fl., *Ravelonarivo 1990* (P scan); forêt de Sorata, 1394 m, 1 Oct 2007, fl., *Razakamalala 3639* (K!, P scan).

Bakerella parvibracteata (Lecomte) Jongkind, **comb. nov.** (Figures 3, 9).

Bas.: *Loranthus parvibracteatus* Lecomte, Notul. Syst. (Paris) 4: 40. 1923.

Type: Madagascar, Analamananara, 1300 m, Jun 1919, fl., *Perrier de la Bâthie 12672* [holotype P (barcode P00752422), isotypes P (barcodes P04978506, P04978505, scans)].

Figure 9. *Bakerella parvibracteata* (Lecomte) Jongkind. Flowers and leaves. (By Guy Eric Onjalalaina (Analamanga, Dec 2016)).

Syn.: *Bakerella poissonii* (Lecomte) Balle subsp. *parvibracteata* (Lecomte) Balle, Adansonia, n. s., 4: 116. 1964a.

Short description

Leaf blade narrowly obovate, 2-5 × 0.5-2 cm, with 1-5 merely visible parallel veins ascending from base almost to the apex, apex rounded, petiole 2-5 mm. Inflorescences axillary, fascicles of a few or several flowers, pedicel c. 2 mm long. Calyx 1.5-2 mm long, membranous, collar-shaped, easily falling apart, sometimes a part left as a small cup on the top of the growing corolla bud. Corolla 2.2-3 cm long, smooth (not winged), first yellow to orange-red, later orange-red to dark red, base inflated, lobes slightly reflexed at anthesis. Anthers 3-5 mm long.

Comments

Bakerella parvibracteata resembles *B. alata* by its flower colour, but its calyx is longer and the corolla is not winged. It is found in forests between 1250 and 2200 m elevation from Ambohitantely in the north to Andringitra in the south.

Other specimens studied

MADAGASCAR. P.K. 376 on Route #7, 34 km N of Fianarantsoa, 1250-1260 m, 31 Jan 1975, fl., *Croat 30145* (K!, P scan, WAG!); Ambohitantely, 12 Mar 1930, fl., *Decary 7437* (P scan); Andringitra, 2200 m, Jun 1965, fl., *Morat 1306* (P scan); Tsinjoarivo, 1400 m, Feb 1925, fl., *Perrier de la Bâthie 16939* (P scan); S de l'hameau Maharoaka, dans la Réserve Naturelle Intégrale Andringitra, Marositry, 1650 m, 8 Apr 1997, fl., *Rakotovao 808* (K!, P scan); Andringitra, Belampo, 12 Feb 2007, fl., *Ranarivelo 474* (K!, P scan); Ambalavao, 5 Jun 1951, fl., *Razafimdrakoto 3056* (P scan); Andringitra National Park, 1787 m, 25 May 2004, fl., *Rogers 646* (P scan); Reserve Integrale Andringitra, c 5 km SE of Antanifotsy, 1500 m, 24 Mar 1989, fl., *Schatz 2672* (K!, P scan, WAG!).

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REFERENCES

Balle S. 1964a. Les Loranthacées de Madagascar et des archipels voisins. Adansonia. ser. 2, 4: 105-141.

Balle S. 1964b. Loranthacées. In: Humbert H. (Ed.), Flore de Madagascar et des Comores 60.

Callmander MW, Luino I, Da-Giau S, Rakotovao C, Gautier L. 2014. A synoptic revision of the Malagasy endemic genus *Socratina* Balle (Loranthaceae). Candollea. 69: 65-73. https://doi.org/10.15553/c2014v691a7

Lecomte H. 1923. Loranthacées de Madagascar. Notulae systematicae (Paris). 4: 34-46.

Thiers B. (continuously updated). Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. Available from: http://sweetgum.nybg.org/ih/ (Accessed May 2025).

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Plagiosiphon intermedium (Leguminosae, Detarioideae), a new tree species from the Ngovayang forest in Cameroon

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Abstract. *Plagiosiphon intermedium* Burgt, Ngansop & Tchiengué, Leguminosae–Detarioideae, is described and illustrated. It is a tree, to 34 m high, with a stem to 66 cm diameter. The leaves have (2 –)3–4(– 5) pairs of opposite leaflets, with the lowest pair often sub-opposite. The flowers are unknown. The fruit is a pod, brown, the valves more or less obovate in outline, 7–9.5 × 3.5–4.5 cm, without visible veins outside, short dense hairy outside. *Plagiosiphon intermedium* occurs in primary rain forest, at 760–870 m elevation. The tree species is endemic to the Ngovayang Massif in the South Region of Cameroon. Three herbarium collections have been made, in an extent of occurrence of only 0.51 km^2. *Plagiosiphon intermedium* is provisionally assessed as Endangered B1(iii,v)+B2(iii,v).

Keywords: Africa, endemic, Fabaceae, Leguminosae, *Plagiosiphon*, endangered.

INTRODUCTION

Plagiosiphon Harms is a genus in the Leguminosae family. The genus was published in 1897, with the species *Plagiosiphon discifer* Harms; followed in 1899 by a more detailed description of the genus and species, (Harms 1897, 1899). In 1951, J. Léonard transferred to *Plagiosiphon* four species from other Detarioideae genera: *P. emarginatus* (Hutch. & Dalziel) J.Léonard; *P. gabonensis* (A.Chev.) J.Léonard; *P. longitubus* (Harms) J.Léonard and *P. multijugus* (Harms) J.Léonard. There exist five accepted species and no synonyms (GBIF 2025; IPNI 2025; POWO 2025). The five accepted species can be distinguished by the key in Léonard 1951: p. 425. The five species of *Plagiosiphon* are rain forest trees and riverine forest trees. *Plagiosiphon emarginatus* occurs in West Africa: Guinea, Sierra Leone, Liberia and Ivory Coast; all five species occur in Central Africa: Cameroon, Equatorial Guinea, Gabon and Congo (Brazzaville).

Plagiosiphon is placed in the Leguminosae subfamily Detarioideae, a subfamily occurring in Cameroon with 42 genera and several hundreds of species (GBIF 2025), mainly in rain forest habitats. The canopy of African rain forests may be dominated by several Detarioideae tree species in co-dominant stands (Aubréville 1968a; Letouzey 1968). Most of the Detarioideae tree species in Korup National Park in Cameroon, including *Plagiosiphon longitubus*, were recorded to occur in groups ranging in size from 50 m to over 1000 m, depending on the species. Groups usually had circular shapes, caused by ballistic seed dispersal. In a group, trees were always mixed with trees of several other Detarioideae species and many trees and tree species from other families (Burgt et al. 2021). The seeds of most Detarioideae tree species are dispersed to relatively short maximum distances, which makes these species poor re-colonisers of forest after disturbance (Letouzey 1960, 1968). Rain forests rich in Detarioideae trees and tree species are supposed to have not been subject to substantial human and natural impacts in historic or prehistoric times (Burgt et al. 2021).

A collection of twigs with leaves, pods, and seedlings from a tree in the Ngovayang Massif in Cameroon, made in 2017 by two of the co-authors of the present study, was determined by the authors to belong to the genus *Plagiosiphon*. The authors were able to return to the tree in 2019, but the tree, and four more trees of the same species standing nearby, were sterile. The authors have not seen any flowering plants. The authors also could not find an existing flowering herbarium collection of this species. The leaves of the specimens differ from those of the other five species of *Plagiosiphon*. The new species of *Plagiosiphon* is here described.

MATERIALS AND METHODS

Herbarium sheets from the herbaria BR, K, MO, P, WAG, YA were studied. All cited material was seen, as an herbarium specimen and/or as an image. The distribution map was made with Simplemappr (Shorthouse 2010). The morphological terminology follows that of Beentje (2016). A preliminarily IUCN extinction risk category was determined following IUCN criteria (2012, 2024).

RESULTS AND DISCUSSION

The genus *Plagiosiphon* currently contains six species. The genus characteristics are in the flowers (Aubréville 1968b, 1970; Harms 1899; Léonard 1951) and are briefly described in the notes section below. The leaves of *Plagiosiphon* are characterised by the distinctive pustulate lower leaflet surface and the emarginate leaflet apex. The six species can be distinguished by the number of pairs of leaflets, and by the shape of these leaflets. The key in Léonard 1951, page 425, distinguishes five species, while the new species *Plagiosiphon intermedium* has a number of pairs of leaflets, (2 –) 3–4 (– 5) pairs, that is unique in the genus.

Plagiosiphon intermedium Burgt, Ngansop & Tchiengué, **sp. nov.** (Figure 1).

Type: Cameroon, South Region, northeast of Bipinde, north of village Ngovayang II, Ngovayang hills, 3°17’26.6’’N, 10°37’1.5’’E, 760 m, fr., 10 Oct. 2017, *Burgt, Grall & Ngansop* 2139 (holotype YA, isotypes K001286582, P, WAG). (Figures 1–4).

Diagnosis

Plagiosiphon intermedium morphologically resembles *Plagiosiphon longitubus* (Harms) J.Léonard; a species from Cameroon, Equatorial Guinea, and Gabon. *Plagiosiphon longitubus* has 4–8 pairs of leaflets; *P. intermedium* has (2 –) 3–4 (– 5) pairs of leaflets. In the Leguminosae subfamily Detarioideae, such a difference in leaflet numbers clearly indicates a difference at the species level.

Description

Tree, to 34 m high, stem to 66 cm diameter. Bark smooth, bright brown, lenticels numerous, lighter in colour than the bark. Twigs glabrous, lenticels in the same colour as the twig. Stipules 2–5 mm long, glabrous, base triangular, apex linear, caducous. Leaves alternate, distributed evenly along the twig, internodes 1–5 cm long. Leaves paripinnate, from 5 × 3 cm to 15 × 8 cm, petiole 0.4–1.2 cm long, rachis 3–10 cm long, canaliculate, petiole and rachis glabrous; leaflets in (2–)3–4(–5) pairs, opposite with the lowest pair often sub-opposite, petiolules up to 0.5 mm long or leaflets subsessile, glabrous; leaflets unevenly elliptic or ovate, to rhombic, apex deeply emarginate, the distal side of the apex longer than the proximal side; the proximal pair of leaflets of a leaf is usually the smallest, the distal pair the largest, distal and middle leaflets 3–8 × 1–2.5 cm, proximal leaflets 2–6 × 0.8–2 cm; leaflet blade glabrous on both sides, primary vein prominent and glabrous on both sides, 12–18 pairs of secondary veins, venation prominent above, faint below; 0–4 glands, visible with a hand lens on the lower surface of the leaflet, positioned on the distal half, near the petiolule, between the primary vein and the edge, sometimes present on the lower and middle leaflets, absent on the upper pair of leaflets. Inflo-

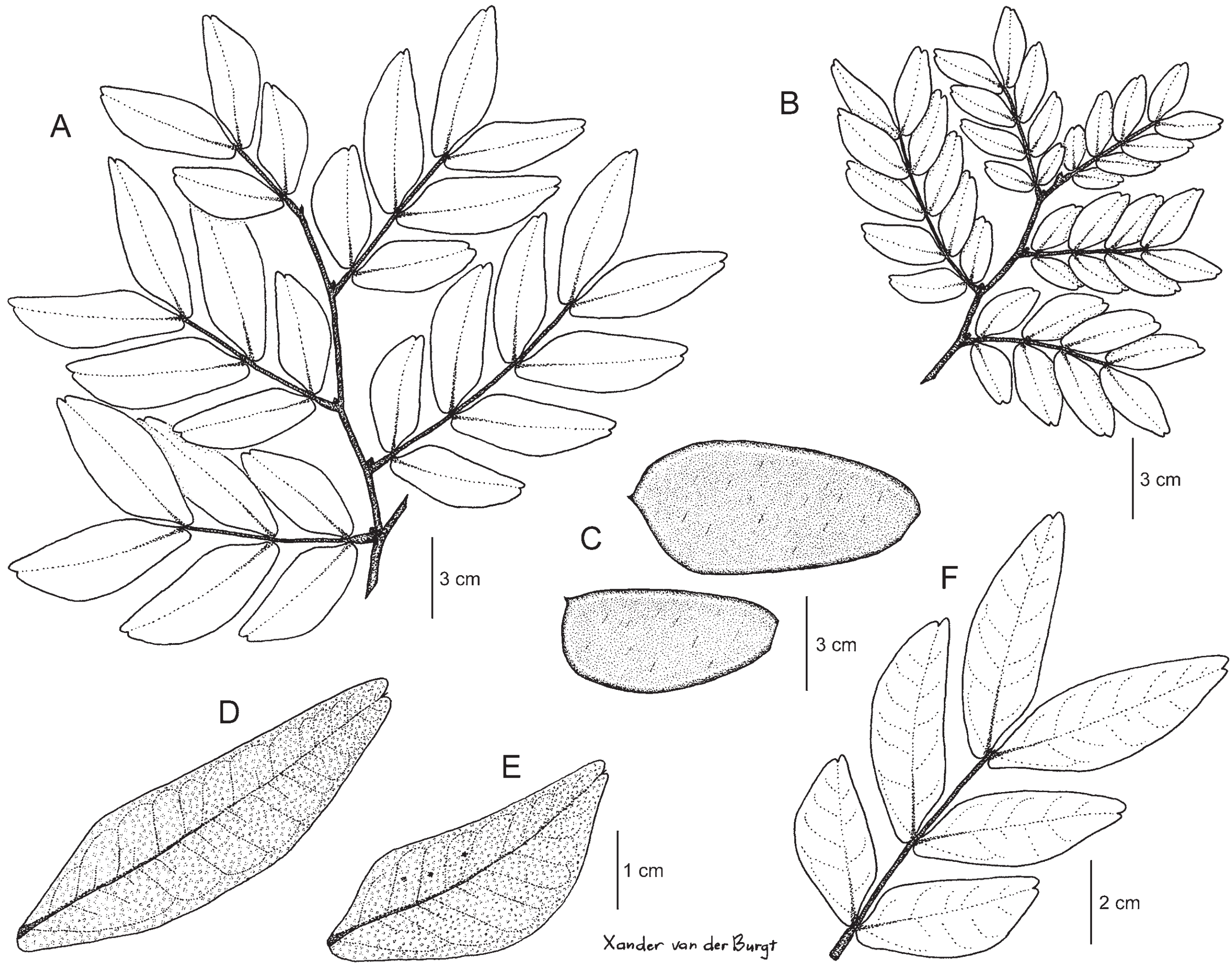


Figure 1. *Plagiosiphon intermedium*. **A.** Branch with large leaves with 2–4 pairs of leaflets. **B.** Branch with small leaves and 4–5 pairs of leaflets, drawn on the same scale as A. **C.** Two pod valves. **D.** Distal leaflet lower side. **E.** Proximal leaflet lower side, with 3 glands. **F.** Leaf with 3 pairs of leaflets. A. from *Burgt* 2387 (K, YA), B. from *Thomas* 3423 (YA), C–F. from *Burgt* 2139 (K, YA). Drawing by Xander van der Burgt.

rescence, flowers, and infructescence unknown. Fruit a pod, woody, dehiscent, brown, valves elliptic to obovate in outline, 7–9.5 × 3.5–4.5 cm, smooth, without visible veins outside, short dense hairy outside, apex acuminate, 2–3 mm long; fruit containing 1–3 seeds; seeds probably ellipsoid, c. 12 cm diameter. Seedling hypocotyl 10–13 cm long, epicotyl 5–8 cm long, first pair of leaves opposite, with 3–4 pairs of leaflets each, leaflets opposite with lowest pair often sub-opposite, leaflets 2–5 × 0.8–1.8 cm.

Etymology

The genus name *Plagiosiphon* is derived from the Greek words "*plagios*" and "*siphon*", and refers to the shape of the receptacle, which has the shape of a tube, "*siphon*", but is oblique, placed at an angle to the symmetric plane, placed sideways, "*plagios*" (Quattrocchi 1999). The species *intermedium* was given that name because of the number of leaflets, which is intermediate between the number of leaflets of *P. discifer* and *P. longitubus*. The other three species of *Plagiosiphon* have a higher number of leaflets. A local name has not been recorded.

Distribution

Plagiosiphon intermedium occurs in Cameroon, South Region, in the Ngovayang Massif (Map 1). The species may also occur on nearby forested hills.

Habitat

Plagiosiphon intermedium occurs in primary rain forest, at 760–870 m altitude.

Figure 2. *Plagiosiphon intermedium.* Stem of a tree 66 cm in diameter at 1.3 m height. From *Burgt* 2139. Another photo of this tree: Murphy et al. 2023, p. 242. Photo by Xander van der Burgt.

Figure 3. *Plagiosiphon intermedium*. Twig with leaves and two pod valves. From *Burgt* 2139. Photo: Xander van der Burgt.

Figure 4. *Plagiosiphon intermedium* seedlings. From *Burgt* 2139. Photo: Xander van der Burgt.

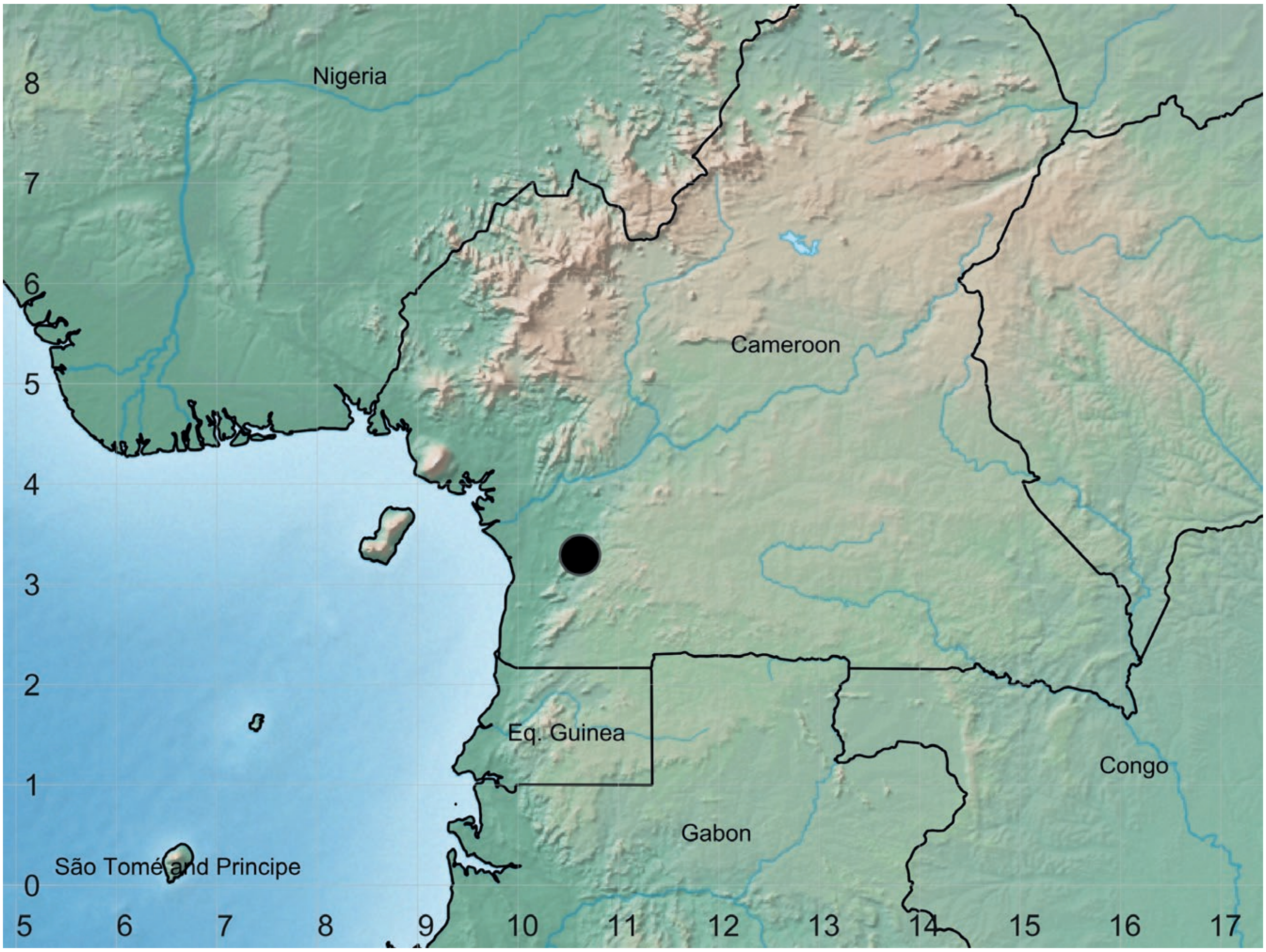
Ecology

Plagiosiphon intermedium was found growing in a group, a characteristic feature of many Detarioideae tree species. This group has a size of at least 400 m × 120 m, and consists of mature trees, saplings and seedlings; mixed with many trees of other species.

Conservation status

The extent of occurrence of *Plagiosiphon intermedium* is 0.51 km^2. This was calculated using the coordinates of the 3 herbarium collections and the 2 observations described on the label of *Burgt* 2387. The area of occupancy of these 5 collections and observations is 8 km^2. The extent of occurrence and area of occupancy should not only include the actually known sites, but also inferred or projected sites (IUCN 2024: p. 53). *Plagiosiphon intermedium* occurs without doubt in more localities in Ngovayang, since on Google Earth there is visible an area of 360 km^2 of potentially suitable forest habitat of over 500 m altitude, within and near the extent of occurrence. It is not detectible whether this is primary forest; parts of it may be secondary forest, where most Detarioideae species occur less abundantly. The actual extent of occurrence may be estimated as more than 100 km^2, but less than 5000 km^2. The actual area of occupancy may be estimated as more than 10 km^2, but less than 500 km^2.

Plagiosiphon intermedium may also occur on nearby forested hills such as the Campo-Ma'an National Park about 50 km to the south, or the Ebo Forest approximately 100 km to the north. Although the level of botanical survey in both areas is far from complete, for this assessment, we assume that *P. intermedium* does not occur there. It is estimated that there are two



Map 1. Distribution of *Plagiosiphon intermedium.*

locations, because the species was found in the forest behind two different villages. Five trees of *Plagiosiphon intermedium* over 12 cm stem diameter, presumably mature trees, were seen during the collecting of *Burgt* 2139 and 2387, in primary forest in a valley bottom and on a steep slope. It is estimated that there exist more than 250 mature trees. Secondary forest was seen at 750 m to the southeast, at 630 m altitude. Because of the presence of secondary forest nearby, where *P. intermedium* may have also occurred, it is likely that there has been decline in quality of habitat and in the number of mature individuals.

The Ngovayang Massif is rich in iron ore, with the highest concentrations of iron located above 750 m (Droissart et al. 2019). Prospection for iron ore may have already caused decline in numbers of mature individuals of *P. intermedium*, and the decline in the future is potentially large. Therefore, *Plagiosiphon intermedium* is here preliminarily assessed as Endangered B1(iii,v)+B2(iii,v).

Notes

The Ngovayang Massif is located in the South Region of Cameroon, and is about 55 km long and 15 km wide. It is covered by lowland and sub-montane rainforest at 100 to 1110 m elevation (Droissart et al. 2019). A dataset of 6116 georeferenced herbarium specimens was compiled; about half of these are from the earliest botanical explorer of the area, the German botanist Georg August Zenker (1855–1922), who collected c. 3000 specimens at "Bipindi" at the southern end of the Ngovayang Massif (Droissart et al. 2019). The Ngovayang Massif represents an Important Plant Area of Cameroon as confirmed by its exceptional plant diversity, by the concentration of many threatened and/or restricted range species as well as by the threat on rare habitats such as the sub-montane vegetation above 750 m elevation (Droissart et al. 2019; Murphy et al. 2023). The Ngovayang forests have some of the highest species' richness and endemism of all Central African forests (Gonmadje et al. 2011; Droissart et al. 2019). Ngovayang contains about 1500 vascular plant taxa (Droissart et al. 2019). The Ngovayang Massif holds the entire global populations of 16 plant species and one subspecies; in other words, 17 taxa are strict endemics of the massif (Murphy et al. 2023). The Ngovayang Massif represents the third richest plant diversity documented area for Cameroon after Mt Cameroon National Park and the Kupe, Mwanenguba and Bakossi mountains (Droissart et al. 2019; Murphy et al. 2023). Topography, high precipitation and permanence of forest cover during periods of drier climate may help explain this richness (Gonmadje et al. 2011). A particular richness in Leguminosae-Detarioideae likely indicates that the area has remained under forest cover during the past ice ages. The new species *Plagiosiphon intermedium* occurs in the Ngovayang Important Plant Area in Cameroon. These two publications advise increased protection of the vegetation of the Ngovayang Massif, by local communities as well as the Cameroon government.

In addition to *Plagiosiphon intermedium*, *P. longitubus* and *P. multijugus* also occur in Ngovayang (Droissart et al. 2019). *Plagiosiphon discifer* probably occurs there as well, because this species was found in two places very near Ngovayang. Flowers of *Plagiosiphon intermedium* have not yet been collected. The flowers probably have the same structure as those of the other species of *Plagiosiphon* (as described in Aubréville 1968b, 1970; Harms 1899; Léonard 1951). If so, these flowers have 2 bracteoles that do not enclose the flower in bud, a receptacle that is elongated, funnel-shaped to cylindrical in shape and gibbous at the base, 4 sepals, (4 –) 5 petals unequal in size, and (8 –) 10 stamens. The three collections of *Plagiosiphon intermedium* show variation in numbers and sizes of leaflets. *Thomas* 3424 has 4–5 pairs of leaflets of 2–3.5 cm long. *Burgt* 2139 and 2387 have 2–4 pairs of leaflets of 3–8 cm long. *Thomas* 3424 consists of leaves from a windfall branch, presumably these are leaves from the canopy, which were positioned in full sunshine. *Burgt* 2139 and 2387 were collected from the lowest branches of the trees, using a pole pruner; these are leaves adapted to half shade. This may explain the variation in numbers and sizes of leaflets between the three collections.

Additional specimens examined

CAMEROON. South Region, northeast of Bipinde, northwest of village Ngovayang II, Ngovayang hills, 3° 17' 23.3" N, 10° 37' 4.0" E, 770 m, sterile, 14 Dec. 2019, *Burgt, Alvarez & Ngansop* 2387 (B, BR, BRLU, EA, FT, G, K, LISC, MA, MO, P, PRE, S, SCA, WAG, YA); steep hillside on Ngovayang Mountain, above Bibondi village, near Lolodorf. 3° 18' N, 10° 39' E, 500–1000 m, sterile, 9 April 1984, *D.W. Thomas* 3424 (K, MO, YA).

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REFERENCES

Aubréville A. 1968a. Les Césalpinioidées de la flore Camerouno Congolaise. Adansonia, sér. 28(2): 147–175.

Aubréville A. 1968b. Flore du Gabon 15, Légumineuses–Césalpinioidées. Muséum National d'Histoire Naturelle, Paris, 362 p.

Aubréville A. 1970. Flore du Cameroun 9, Légumineuses–Césalpinioidées. Muséum National d'Histoire Naturelle, Paris, 339 p.

Beentje H. 2016. The Kew plant glossary, an illustrated glossary of plant terms, ed. 2. Royal Botanic Gardens, Kew.

Burgt X.M. van der, Newbery D.M., Njibili, S. 2021. The structure of Leguminosae-Detarioideae dominant rain forest in Korup National Park, Cameroon. Plant Ecology and Evolution. 154(3): 376–390. https://doi.org/10.5091/plecevo.2021.1879

Droissart V., Lachenaud O., Dauby G., Dessein S., Kamdem G., Nguembou KC., Simo-Droissart M., Stévart T., Taedoumg H. & Sonké B. 2019. Mine versus Wild: a plant conservation checklist of the rich Iron-Ore Ngovayang Massif Area (South Cameroon). Plant Ecology and Evolution. 152(1): 8–29. https://doi.org/10.5091/plecevo.2019.1547

GBIF.org (2025), GBIF Home Page. Available from: https://www.gbif.org [Retrieved 16 Aug. 2025]

Gonmadje C, Doumenge C, Sunderland TCH, Balinga M, Sonké B. 2012. Analyse phytogéographique des forêts d'Afrique Centrale: le cas du massif de Ngovayang (Cameroun). Plant Ecology and Evolution. 145(2): 152–164. https://doi.org/10.5091/plecevo.2012.573

Harms H. 1897. Leguminosae. In: Engler A, Prantl K. (Eds.), Naturlichen Pflanzenfamilien Nachträge I.: 190–204.

Harms H. 1899. Leguminosae africanae II. In: Engler A. (Ed.), Botanische Jahrbücher fur Systematik. 26: 253–324.

IPNI 2025. International Plant Names Index. Published on the Internet http://www.ipni.org The Royal Botanic Gardens, Kew, Harvard University Herbaria & Libraries and Australian National Herbarium. [Retrieved 1 August 2025].

IUCN 2012. IUCN Red List categories and criteria. Version 3.1. Second edition. Prepared by the IUCN Species Survival Commission. IUCN, Gland & Cambridge. https://www.iucnredlist.org/resources/categories-and-criteria

IUCN 2024. Guidelines for Using the IUCN Red List categories and criteria. Version 16. Prepared by the Standards and Petitions Committee of the IUCN Species Survival Commission. Published at https://www.iucnredlist.org/resources/redlistguidelines

Léonard J. 1951. Notulae systematicae XI. Les *Cynometra* et les genres voisins en Afrique tropicale. Bulletin du Jardin botanique de l'étatcBruxelles. 21(3/4): 373–450. https://doi.org/10.2307/3666679

Letouzey R. 1960. La forêt à *Lophira alata* Banks du littoral camerounais. Hypothèses sur ses origines possibles. Bulletin de l'Institut d'Études Centrafricaines. 19–20: 219–240.

Letouzey R. 1968. Etude phytogéographique du Cameroun. Lechevalier, Paris. https://doi.org/10.5962/p.296414

Murphy B, Onana J-M, Burgt X van der, Ngansop Tchatchouang E, Williams J, Tchiengue B, Cheek M. 2023. Important Plant Areas of Cameroon. Royal Botanic Gardens, Kew. 302 pp. https://kew.iro.bl.uk/concern/books/c056b5cb-b146-4509-b98b-a7f5dd49517e

POWO (2025). Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet; https://powo.science.kew.org/ [Retrieved 16 August 2025].

Shorthouse DP. 2010. SimpleMappr, an online tool to produce publication-quality point maps. Retrieved from https://www.simplemappr.net [Accessed January 19, 2025].

Quattrocchi U. 1999. CRC World Dictionary of Plant Names: common names, scientific names, eponyms, synonyms, and etymology. Vol. 3. CRC Press.

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Keetia tinka & *K. kounounkan* sp. nov. (Rubiaceae - Vanguerieae) new threatened forest climbers and shrubs of sandstone plateaux of the Republic of Guinea

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Abstract. Two new species of *Keetia* are described from recent botanical collections for conservation management made in surviving submontane forest areas of the sandstone plateau areas of the Republic of Guinea. *Keetia kounounkan* Cheek & Simbiano is a shrub of the Kounounkan Plateau towards the border of Sierra Leone, so far with a single location in gallery forest. *K. tinka* Cheek & Simbiano is an evergreen rainforest climber of the main part of the Fouta Djalon Highlands with two locations both in degraded forest. Both species are described, illustrated and provisionally assessed for their conservation status, the first as Critically Endangered, the second as Endangered.

Keywords: conservation, *Keetia*, lianas, Rubiaceae, taxonomy.

INTRODUCTION

Keetia E.Phillips (Rubiaceae, Vanguerieae) was segregated from *Canthium* Lam. by Bridson (1985, 1986). This genus of about 41 accepted species (Cheek and Onana 2024) is restricted to sub-Saharan Africa (excluding Madagascar and the Mascarene Islands) and extends from Senegal and Guinea in West Africa (Gosline et al. 2023a, 2023b) to Sudan (Darbyshire et al. 2015) in the North and East, and S. Africa in the South (Bridson 1986). *Keetia* differs from other African genera of Vanguerieae by its pyrenes with a fully or partly-defined lid-like area around a central crest, and the seed endosperm with tanniniferous areas (Bridson 1986). *Keetia* species are usually climbers (very rarely shrubby) and occur mostly in forest habitats, but sometimes in wooded grassland. In a phylogenetic analysis of the tribe based on morphology, nuclear ribosomal ITS and chloroplast *trnT-F* sequences, Lantz and Bremer (2004), found that based on a sample of four species, *Keetia* was monophyletic and sister to *Afrocanthium* (Bridson) Lantz & B. Bremer with strong support. Highest species diversity of *Keetia* is found in Cameroon and Tanzania, both of which have about 15 taxa (Onana 2011; POWO, continuously updated) and in Gabon, where 10 species are currently recorded (Sosef et al. 2006) but around 25 are actually present, many of them undescribed (Lachenaud pers. comm. to Cheek, 2024). Recently, bacterial leaf nodulation was discovered to occur in the genus, making Vanguerieae the fourth tribe and only the fourth genus of the family in which this is recorded, (Cheek and Onana 2024). Several *Keetia* species are point endemics, and have been prioritized for conservation (e.g. Onana and Cheek 2011; Couch et al. 2019; Murphy et al. 2023) and one Guinean threatened species, *Keetia susu* Cheek has a dedicated conservation action plan (Couch et al. 2022).

Bridson's (1986) account of *Keetia* was preparatory to treatments of the Vanguerieae for the Flora of Tropical East Africa (Bridson and Verdcourt 1991) and Flora Zambesiaca (Bridson 1998). Pressed to deliver these, she stated that she could not dedicate sufficient time to a comprehensive revision of the species of *Keetia* outside these areas: "full revision of *Keetia* for the whole of Africa was not possible because the large number of taxa involved in West Africa, the Congo basin and Angola and the complex nature of some species would have caused an unacceptable delay in completion of some of the above Floras. [...] A large number of new species remain to be described." (Bridson 1986). Several of these new species were indicated by Bridson (1986), and other new species by her arrangement of specimens in folders that she annotated in the Kew Herbarium. One of these species was later taken up and published by Jongkind (2002) as *Keetia bridsoniae* Jongkind. In the same paper, Jongkind discovered and published *Keetia obovata* Jongkind. Based mainly on new material, additional new species of *Keetia* have been published by Bridson and Robbrecht (1993), Bridson (1994), Cheek (2006), Lachenaud et al. (2017), Cheek et al. (2018a), Cheek and Bridson (2019), Cheek and Onana (2024), Cheek et al. (2024a), Cheek et al. (2024b) and there are several other specimens that fit no other species, (e.g. Cheek et al. 2004; 2011) and remain to be described.

In this paper we continue the project towards an updated taxonomic account of *Keetia* by describing from recently collected material two further new species from Guinea, *K. tinka* Cheek & Simbiano (previously considered to be a variant of *K. magassoubiana* Cheek) and *K. kounounkan* Cheek & Simbiano (initially identified as *K. susu*). Despite both species lacking flowers there is clear supporting diagnostic evidence to justify recognition.

In recent years, numerous new species to science have been described from Guinea, such as from the surviving remnants of species-diverse forests. These include species of climbers e.g. in *Monanthotaxis* Baill. (Annonaceae, Hoekstra et al. 2021), *Hibiscus* L. (Malvaceae, Cheek et al. 2020a), *Keita* Cheek (Olacaceae, Cheek et al. 2024c), small trees and shrubs e.g. *Casearia* Jacq. (Salicaceae, Breteler and Baldé 2024), *Tarenna* Gaertn. (Rubiaceae, Jongkind 2021), and *Tabernaemontana* L. (Apocynaceae, Jongkind & Lachenaud 2022), non-chlorophyllous heteromycotrophs (*Gymnosiphon* Blume, Burmanniaceae, Cheek et al. 2024d) and from waterfalls, rheophytes e.g. *Inversodicraea* Engl. and *Saxicolella* Engl. (Cheek et al. 2017; 2022). These discoveries are set to continue so long as funds to support taxonomists and taxonomic work continues and habitat survives.

MATERIALS AND METHODS

Names of species and authors follow IPNI (continuously updated) and nomenclature follows Turland et al. (2018). Herbarium material was collected using the patrol method e.g. Cheek and Cable (1997) and processed and studied as in Davies et al. (2023). Herbarium specimens were examined with a Leica Wild M8 dissecting binocular microscope fitted with an eyepiece graticule measuring in units of 0.025 mm at maximum magnification. The drawing was made with the same equipment with a Leica 308700 camera lucida attachment. Pyrenes were characterized by simmering selected ripe fruits in water until the flesh softened and could be removed by scalpel. A toothbrush was then used to clean the pyrene surface to expose the surface sculpture and the lid. Finally, a fine saw was used to cut a transverse section of the fruit and seed, allowing observation of tanniferous cells in the seed endosperm and measurement of the endocarp thickness. Specimens were inspected from the following herbaria: BM, FHO, HNG, K, P, SL and YA and images of specimens on Gbif.org.

Google Earth Pro was used to view the collecting sites, read accurate elevations, to assess the continued survival of the species using as proxy the continued existence of forest habitat at the collection site, and also to evaluate likely extent of occurrence sensu IUCN (2012) for the conservation assessment. The format of the description follows those in other papers describing new species of *Keetia*, e.g. Cheek et al. (2025). Terminology follows Beentje and Cheek (2003). All specimens indicated "!" have been seen. The conservation assessment follows the IUCN (2012) standard. Herbarium codes follow Index Herbariorum (Thiers, continuously updated).

TAXONOMIC TREATMENT

The first of the two new species, *Keetia kounoukan,* had been initially identified as the locally more frequent *K. susu* to which it is superficially similar, also being a large-fruited shrub or small tree of sandstone habitats in Guinea. However, on closer examination it was found to differ in so many unusual character traits that it is not clear with which species in the genus its closest affinities are with (Table 1 below). In the key to the *Keetia* species of West Africa (Cheek et al. 2025) it fits neither of the leads in the first couplet, having patent brown hairs on the stem > 0.5 mm long. Although the fruits resemble those of *K. susu* and its allies, they lack the greatly accrescent disc, and the pyrene lid and sculpture are completely different (Table 1).

Keetia kounounkan Cheek & Simbiano, **sp. nov**., (Figures 1, 2, 3).

Type: Guinea, Forécariah Prefecture, southern plateau of Kounounkan Massif, 9° 33’ 01.6” N 12° 50’ 20.4” W, 1100 m, fr., 5 Feb. 2019, *van der Burgt 2262* with *P.M. Haba, Konomou & Xanthos* [holotype K! (barcode K001971152); isotypes BR, HNG (barcode 0002731)].

Diagnosis

Keetia kounounkan is similar to and was initially identified as *Keetia susu* Cheek but *K. susu* has a glabrous petiole, (the petiole of *Keetia kounounkan* is densely hairy). The leaf acumen of *K. susu* is acuminate, with a sharp point, while in *K. kounounkan* the acumen has a rounded apex. The domatia of *K. susu* are pit domatia, hairy within the pit only, while the domatia of *K. kounounkan* are tuft domatia with exserted hairs. The fruits of *K. susu* are larger, 13–17 × 15–20 × 11–13 mm, glossy black when ripe, while the fruits of *K. kounounkan* are smaller, 10 x 11–12 x 6–7 mm, brown when ripe. The fruit disc of *K. susu* is 5–8 mm in diameter, while the fruit disc of *K. kounounkan* is 1–3 mm in diameter. See Table 1 for additional diagnostic characters.

Description

Shrub, 2 m high, 4 m wide, stem to 5 cm thick at base. Primary stems erect, not climbing, secondary shoots ascending, stout, bearing usually two pairs of leaves at stem apex, fruiting from leafless nodes. Leafy stems cylindrical, drying grey to black, internodes 2–4.5 cm long, lenticels inconspicuous, young stems densely hairy, hairs simple, persisting to the third node from the apex, brown, straight, stout, acute, appressed to subappressed, 0.2–0.9 mm long, extending to the petiole, abaxial midrib, secondary veins, margins of leaf-blades, and the infructescence axes, older stems glabrescent. Stipules persistent to the third node, glabrescent, 7–12 mm long, base broadly triangular, 2–4 mm long, 4–8 mm wide; midrib keeled, extended as a straight, stout awn 5–8 mm long, apex acute; colleters in a line inside at the base of the stipule, 0.1–0.2 mm long, mixed with much longer simple hairs 0.2–0.5 mm long. Leaves on primary stem not seen; secondary stem leaves simple, opposite, equal, thickly leathery, matt, drying pale green above, whitish green below; petiole canaliculate 5–10 mm long, 2–3 mm wide, densely hairy (hairs as stem), hairs to 0.5 mm long, Leaf blade elliptic, 8.8–10.5 x 4.7–6.3 cm, acumen 3(– 7) mm long with rounded apex, base broadly acute to subtruncate, leaf edges a little decurrent on petiole, primary vein and secondary veins somewhat raised on the upper surface, clearly raised on the lower surface, with sparse brown hairs to 0.6 mm long, secondary veins 5–6 on each side of the midrib, arising at

Table 1. Selected diagnostic characters separating *Keetia kounoukan* from *K. susu*

	Keetia susu	*Keetia kounounkan*
Petiole length and indumentum	4–16 mm, glabrous	5–10 mm, densely hairy
Leaf acumen apex	Acute	Rounded
Domatia	Pit domatia (hairs inside pit)	Tuft domatia (hairs exserted)
Fruit size and colour	13–17 × 15–20 × 11–13 mm, glossy black when ripe	10 × 11–12 × 6–7 mm, matt brown when ripe
Fruit disc	5–8 mm in diameter	1–3 mm in diameter
Pyrene lid and pyrene surface sculpture	Lid ventral, lacking crest; pyrene surface with irregular raised areas.	Lid apical, indistinct, crest with midline furrow; surface smooth, with fingerprint pattern (Fig 1K)
Stipule awn length	4–4.5 mm	4–8 mm
Stem habit, indumentum	Primary stems scandent (young plants), some secondary shoot pairs reflexed, glabrous.	Primary stems not scandent (even in young plants), secondary shoots ascending, densely hairy (distal internodes).

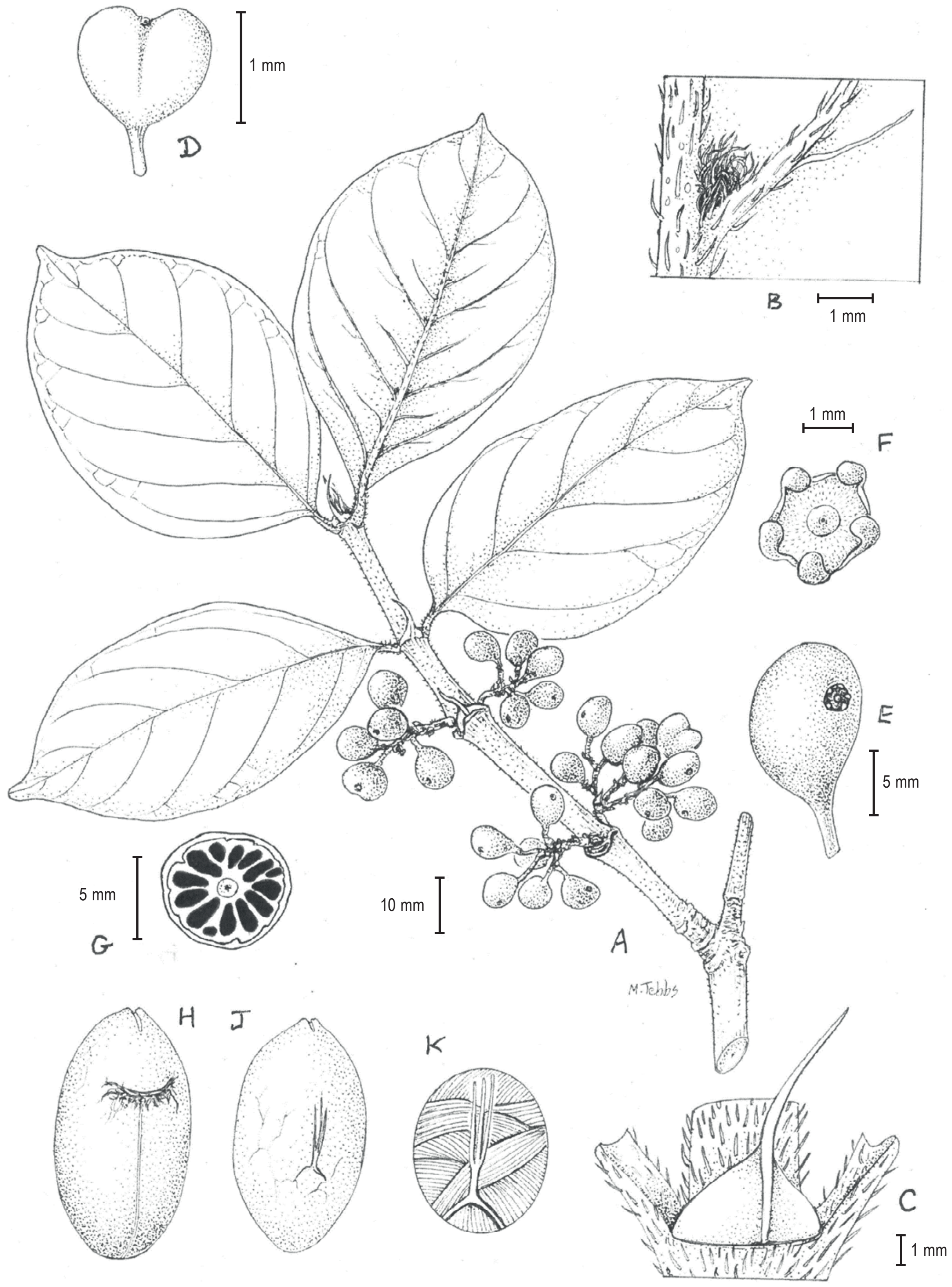

Figure 1. *Keetia kounounkan* Cheek & Simbiano - **A.** secondary stem with infructescences; **B.** domatium, on lower leaf surface; **C.** stipule; **D.** 2-seeded fruit; **E.** 1-seeded fruit; **F.** disc and calyx of a 1-seeded fruit; **G.** transverse section of seed showing tanniniferous rays; **H.** pyrene ventral view; **J.** pyrene dorsal view; **K.** detail of surface of pyrene. All from *van der Burgt* 2262 (K). Drawn by Margaret Tebbs.

40–50°, arching straight then towards margin, forming a weak, looping marginal nerve. Tertiary nerves inconspicuous and sparse. Tuft domatia between the midrib and secondary veins, orbicular to longitudinally elliptic, 1–1.5 mm long, with brown weakly crisped hairs 0.2–0.6 mm long. Inflorescence and flowers not seen. Infructescence axillary, 2.5–3.5 x 2–3.5 cm, with 3–7 fruits, peduncle (2–) 5 mm long, basal bract pair naviculate, 8 x 2 mm, apices awned; rachis bifurcate 1–4 mm from base, branches 5–13 mm long; bracts triangular, 2–3 mm long, 1–2 mm wide at base, apex acuminate to awned, inflorescence axes hairy, hairs brown, to 0.8 mm long. Fruits brown (from green) when ripe, dull, 1- or 2-seeded, bracteoles linear, c. 1 mm long, pedicel 2–3 mm glabrous; 1-seeded fruits ellipsoid 8–12 × 5–9 × 5–7 mm, calyx located at the side of the fruit, 2–3 mm diameter, lobes 5–6, oblong-elliptic 0.4–0.6 x 0.1–0.3 mm, apex hooded, incurved (Fig. 1 F) persistent; disc torus-like to saucer-shaped 0.6–0.8 mm diameter, drying glossy black, glabrous, surrounded by a ring of erect hairs, hairs 0.6 mm long; 2-seeded fruits heart-shaped (retuse and widest at apex, Fig 1 K), 10 x 11–12 x 6–7 mm, a little constricted between the carpels, calyx located in a sinus 1 mm deep between the carpels. Pyrene of 1-seeded fruit pale brown, ellipsoid or slightly reniform, lid shallowly convex, pointing sub vertically 1.5 x 2.5 mm crest shallow, with a longitudinal groove; pyrene of 2-seeded fruit ellipsoid, flattened along 1 side, 10.5 x 5.5 x 5.5 mm. Pyrene wall 0.15–0.3 mm thick, outer surface pale brown with low rounded projections separated by fibres; surface with glassy finger-print-like pattern (Fig. 1 K). Seed as pyrene, 7 × 5 × 4 mm, surface pustulate, dark brown, convoluted; seed in transverse section with endosperm tanniniferous areas dense, black, arranged in 12–14 rays (Fig 1.G), rays separated by bands of hard white endosperm, embryo cylindric, central.

Etymology

The species is named after the Kounounkan plateau, as this is the only place where the species was observed. Kounounkan is of immense importance for plant conservation in view of the number of globally unique and highly threatened species present.

Distribution

GUINEA. Forécariah Prefecture, southern plateau of Kounounkan Massif.

Habitat and ecology

Fissured sandstone rocks, among shrubs and small trees along a seasonal stream close to a sparsely wooded meadow at an altitude of 1100 m. The ecological conditions of this environment are influenced by the presence of seasonal water, which contributes to soil moisture and the diversity of surrounding plant species. In the submontane forest gallery where *Keetia kounounkan* was found, several associated plant species were observed,. These species include *Memecylon afzelii* G.Don, *Hibiscus kounounkan* Cheek ined., *Ternstroemia guineensis* Cheek, *Warneckea fascicularis* (Planch. ex Benth.) Jacq.-Fél., *Ficus ovata* Vahl, *Cailliella praerupticola* Jacq.-Fél., *Glenniea africana* (Radlk.) Leenh., *Kotschya uniflora* (A.Chev.) Hepper, *Keetia mannii* (Hiern) Bridson, and *Keetia susu*.

Individuals are typically scattered and associated with other flora adapted to similar conditions. The specialized nature of this habitat, however, makes the species vulnerable to environmental degradation, including fire and habitat fragmentation.

Conservation status

Keetia kounounkan is an endemic species from Guinea, currently known only from the southern plateau of the Kounounkan Massif in Forécariah Prefecture. Although it is represented by a single herbarium specimen, several other individuals of the species have been observed at the site.

Its extent of occurrence (EOO) is estimated to be no greater than 16 km², based on the area of the southern plateau of the Kounounkan Massif from which the only known collection and observations have been made. Its area of occupancy (AOO) across the plateau area is also likely to be highly restricted but may narrowly exceed 10 km². The plateau isconsidered to represent a single location threatened by dry-season bushfires set by cattle herders. As a result of this threat, the species is inferred to be undergoing a continuing decline in habitat quality. The number of mature individuals cannot be reliably estimated, but it is suspected that the true value may exceed 1,000.

Given the availability of other similar submontane habitats in neighbouring Kindia and Dubréka Prefectures, it is possible that this species occurs at other sites; however, it has not yet been reported from collecting trips to neighbouring plateaux. Pending more precise data on its distribution and population size, and adopting a precautionary approach on the basis that its distribution may prove to be highly restricted, *Keetia kounounkan* is here provisionally assessed as Critically Endangered (CR) B1ab(iii), following IUCN criteria. Further survey work is essential to refine this conservation assessment; for example, confirmation of its presence on other plateaux may permit assessment at a lower category of extinction risk, though it would likely remain threatened.

Figure 2. *Keetia kounounkan* Cheek & Simbiano - In habitat in stunted gallery forest of a seasonal stream set in grassland on the Kounounkan sandstone plateau. *Van der Burgt* 2262. Photo by Xander van der Burgt

Figure 3. *Keetia kounounkan* Cheek & Simbiano - Close up showing the fruits, ripe and unripe (*van der Burgt* 2262). Photo by Xander van der Burgt

Kounounkan was designated as a TIPA (Tropical Important Plant Area) in 2019 (Couch et al. 2019) and is set to become a formally protected area. Of the 22 TIPAs in Guinea it has the highest number of strictly endemic species, with seven globally unique species recorded (Couch et al. 2019), including *Gladiolus mariae* Burgt (Iridaceae, van der Burgt et al. 2019), *Ternstroemia guineenis* Cheek (Ternstroemiaceae, Cheek et al. 2019). Subsequently, some of these species have been found elsewhere, but at the same time, additional new endemic and near endemic species have been published from Kounounkan and nearby sandstone plateaux e.g. the new genus *Benna alternifolia* Burgt & Ver.-Lib. (Melastomataceae, van der Burgt et al. 2022), *Ctenium bennae* Xanthos and *Trichanthecium tenerium* Xanthos (both Poaceae, Xanthos et al. 2020; 2021).

Notes

Among the species of *Keetia* found growing with *Keetia kounounkan, K. mannii* (Hiern) Bridson is morphologically similar but differs in having scandent, glabrous stems (or only a few hairs), leaves with an acute acumen apex, and pit domatia similar to those of *K. susu*. In contrast, *K. kounounkan* has densely pubescent, erect (non climbing)young stems, leaves with a rounded acumen apex, and tuft domatia.

Keetia kounounkan is distinctive in the genus for its non climbing habit (resembling in this *Keetia susu,* although when young that species is scandent) and unusual also for the stiff bristle like hairs on the stems, petiole and abaxial veins of the leaf blade. The persistent stipules, with robust, long awns are also distinctive. The fruit colour, dull brown and matt when ripe is unusual in a genus where fruits are usually red or orange, sometimes black, when ripe. These features make the species readily identifiable despite its initial similarity to *K. susu.*

The apparent rarity of this species highlights the importance of continued research and conservation action to obtain it in flower, and to understand its full distribution, ecological preferences, and conservation needs. The clear morphological distinctions underscore the richness of the genus *Keetia* in Guinea.

The two specimens of the second species described in this paper, *Keetia tinka* (*Balde* 274 and *Fofana* 303) were formerly considered for inclusion as a subspecies of *K. magassoubiana* (formerly *K. sp. aff. tenuifolia* of Bridson, Cheek et al. 2025) until it was found that the number of morphological characters separating them, mainly qualitative (see Table 2) justified species rank. This conclusion is further supported by the different geographic and elevational ranges of the two taxa (Table 2). The two species also bear fruit (and so likely flower also) at different seasons. It seems highly probable that the two taxa are closely related due to the many similarities in all organs that are known for both species e.g. the fruits are almost indistinguishable.

Keetia tinka Cheek & Simbiano, **sp. nov.**

Type: Republic of Guinea, Fouta Djalon, Dalaba Prefecture, Forêt Classée de Tinka, near Karéh, `Edge of secondary forest, disturbed area, old field', 10° 22' 50.0" N

Table 2. Diagnostic characters separating *Keetia magassoubiana* from *Keetia tinka* sp. nov. Data for the first species from Cheek et al. (2025) and specimens cited at K therein.

Characteristic	*Keetia magassoubiana*	*Keetia tinka*
Leaves of secondary stems: shape and base	Narrowly elliptic to oblong, length: breadth ratio 2.5–3.5: 1 Leaf base acute	Elliptic (rarely ovate-elliptic), length: breadth ratio 1.3–2(– 2.25): 1 Leaf base obtuse to rounded
Domatia	Mainly present along midrib. Domed with a minute central aperture c. 0.1 mm diam. Hairs not visible within.	Mainly present at secondary nerve junctions. Open pits, aperture 0.25–0.5 mm wide. Hairs conspicuous within aperture.
Stipule awn	Stipule awn flat, straight	Stipule awn folded along midrib, arched
Peduncle bract pair	United at base, forming a sheath, margins laciniate	Free at base, not forming a sheath, each triangular, margins entire
Pyrene surface	Honeycombed (deeply pitted)	Subverrucate
Seed endosperm in transverse section	Conspicuous radial black tanniniferous bands	Tanniferous cells dispersed, inconspicuous, bands absent
Fruiting season	February to May	July to October
Elevational range (m)	15–960 m	1070–1380 m
Geographic range	Guinea (Guinée Maritime, Haute Guinée, Guinée Forestière), Ivory Coast, Sierra Leone, Liberia	Guinea (Moyenne Guinée)

12° 15' 12.9" W, 1278 m, fr., 19 Oct. 2017, *Fofana F.* 303, with *Larridon, I. Couch, C. & Haomou, A.* [holotype K! (barcode K000874709); isotype HNG]. (Figure 4).

Diagnosis

Keetia tinka is similar to *Keetia magassoubiana* Cheek but differs in the leaf blades elliptic (rarely ovate-elliptic), length: breadth ratio 1.3–2(– 2.25): 1 and with leaf base obtuse to rounded (vs narrowly elliptic to oblong, length: breadth ratio 2.5–3.5: 1, leaf base acute). The domatia of *K. tinka* are mainly present at secondary nerve junctions, they are open pits, aperture 0.25–0.5 mm wide, with hairs conspicuous within the aperture (vs mainly present along midrib, domed, with a minute central aperture c. 0.1 mm diam. And hairs not visible within. The pyrene of *K. tinka* has a subverrucate surface and the seed endosperm in transverse section lacks tanniniferous rays (vs pyrene honeycombed, tanniniferous rays conspicuous).

Description

Lianescent evergreen forest shrub 5–6 m high. Primary stems cylindrical to slightly 4-angular, brown-black, internodes 1–3.5 x 0.2–0.5 cm, glabrous. Secondary stems (plagiotropic brachyblasts), 12.5–17.5 cm long, with 6–9 nodes (Fig 4A), ascending, cylindrical, internodes 1.3–2.7 x 0.1–0.3 cm, hairs very sparse, slightly spreading, white, 0.4–0.6(– 1) mm long (Fig. 4B). Leaves of primary stems unknown, those of secondary stems simple, opposite, equal, blade thinly leathery, pale brownish-green to brownish-grey adaxially, abaxially pale whitish grey after drying, elliptic, less usually ovate-elliptic, (2.75–)3–8 x (1.3–)1.5–4 cm, apex acute to acuminate, with a short acumen 0.2–0.5(– 0.8) cm long, the acumen apex minutely mucronate and hooded (Fig 4E), base obtuse or rounded, sometimes slightly decurrent towards the top of petiole, asymmetrical, margins entire and slightly revolute. The adaxial (upper) surface with a raised midrib and secondary veins, abaxial (lower) surface bearing a few sparse, slightly spreading hairs. The secondary veins bright white, broad, 4 to 6 on each side of the midrib, arise at about 60°, bifurcating c. 5 mm from the margin, the branches uniting (abaxial surface) to form an inconspicuous, weak, looping inframarginal vein, tertiary veins rare and scarcely visible. Domatia absent at the junction of midrib and secondary veins, or rarely present at the most distal nodes (Fig 4F), frequent at the branches of secondary veins (Fig. 4G), domatial pits, orbicular and c. 0.25 mm diam., or longitudinally elliptic, c. 0.5 x 0.25–0.3 mm, containing 5–12 straight orange hairs 0.1–0.3 mm long; indumentum of the midrib (both surfaces) and abaxial secondary veins moderately dense, with appressed, straight, stiff, acute, red-brown hairs, 0.3–0.5 (– 1) mm long; petiole canaliculate, (3–)4–7(– 8) x 0.8–1 mm with adpressed hairs 0.3–0.5 mm long. Stipules more or less persistent until the 4–5 th node from stem apex, 2–7(– 8) x c.2 mm, base triangular, 2–2.2 x 2 mm, (including basal sheath c. 1 mm long) apical awn 5(– 6) x 0.3–0.5 mm, folded in two along the midrib, arched (Fig 4D) apex acute or rounded; external surface with moderately dense hairs c. 0.25–0.3 mm long, adpressed, translucent; inner surface glabrous except for a line of colleters and hairs at the base. Colleters c. 5 per stipule,

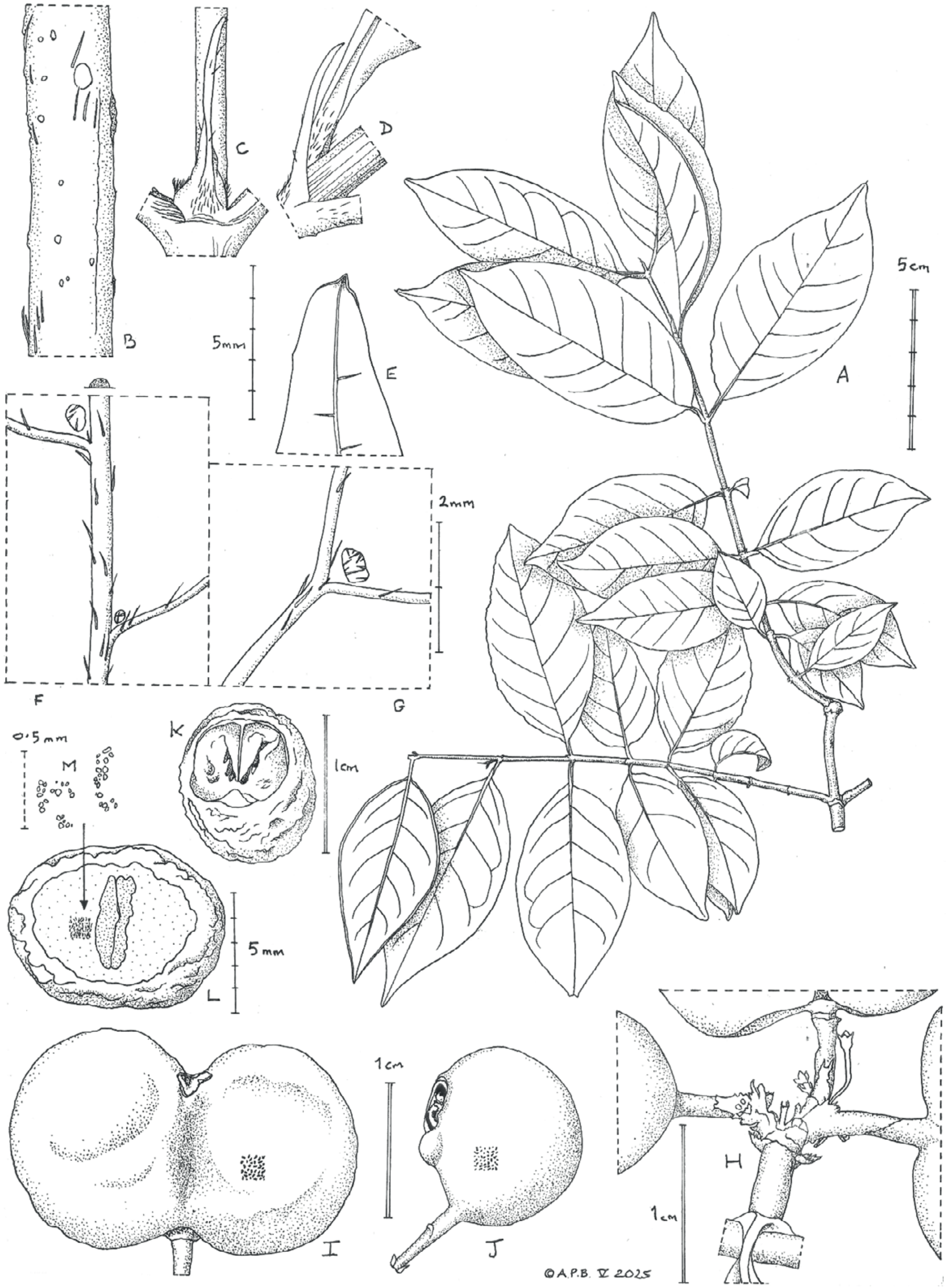

Figure 4. *Keetia tinka* Cheek & Simbiano - **A.** habit, two leafy secondary stems; **B.** secondary stem indumentum; **C.** stipule, face view; **D.** stipule side view, and petioles; **E.** acumen with apical mucro; **F.** midrib domatia (atypically present); **G.** typical domatia of secondary nerve bifurcations; **H.** infructescence axis; **I.** 2-seeded fruit, side view; **J.** 1-seeded fruit, side view; **K.** pyrene showing the flat, ventral lid; **L.** transverse section of seed with collateral cotyledons; **M.** detail of the dispersed, inconspicuous tanniniferous cells of the seed endosperm. A-C, E-I, K. from *Fofana* 303 (K), D, J, L-M. from *Baldé* 274 (K). Drawn by Andrew Brown.

glossy brown or black, erect, conical 0.25–0.3 x 0.1–0.15 mm, exposed when stipules fall; hairs erect, wiry, red, 0.7–1 mm in length. Inflorescence and flowers not seen. Infructescences axillary, subtended by leaves on secondary stems at 2–3 successive or alternating nodes, 2.5–3.5 x 3.9–5 cm, 3–9-fruited, peduncle stout 3–12 mm long, bract pair opposite, inserted c. 2 mm below apex, triangular, 1.5(– 2) x 1.5(– 2) mm, moderately hairy, hairs grey 0.1– 0.3 mm long; rachis glabrous, bifurcate, the branches each bifurcating 2(–3) times, bracts and bracteoles slightly smaller than peduncular bracts. Fruits glossy dark brown after drying, surface smooth, glabrous; 2-seeded fruits (3 of 4 fruits in *Fofana* 303, K) strongly didymous, with a deep furrow on both sides separating the globose carpels, 1.4–1.5 x 2.3–2.5 x 1–1.1 cm, apex and base emarginate, disc distinctly accrescent, 0.3–0.4 cm in diameter, V-shaped (due to carpel expansion), densely hairy, hairs translucent, straight, erect, 0.1–0.2 mm long. Calyx lobes erect, triangular, c. 0.6 x 0.5 mm, inner surface densely hairy, hairs c. 0.1 mm long, sinuous, thick. 1-seeded fruits (all 18 fruits in *Baldé* 274, K) as for 2-seeded fruits, but ellipsoid, 11–15 x 9–13 x 9–12 mm, pedicel attached obliquely, disc lateral, flat, often with an aborted carpel inserted between disc and pedicel; aborted carpel hemi-ellipsoid, c. 3 x 2 mm, 1.5 mm tall. Pyrene ellipsoid, 0.9–1.1 × 0.7–1 x 0.8–1 cm, apex and base broadly rounded, ventral surface slightly convex; lid ventral, nearly flat, semicircular, 6.5 x 7.5 mm, crest indistinct with a cleft along the midline; wall, c.0.5 mm thick; outer surface subverrucate, inner surface smooth and shiny. Seed ellipsoid 9 x 5–5.5 × 4–6 mm, surface convoluted, brain-like, black-brown, in transverse section endosperm with thinly dispersed and inconspicuous tanniniferous cells (bands absent); embryo with two flat cotyledons (Fig. 4K).

Etymology

The species is named after the Tinka forest, Dalaba, as this is where the species appears to have the best possibility of surviving.

Phenology

Fruiting July–October.

Distribution

Guinea, Fouta Djalon, Dalaba Prefecture, Forêt classée de Tinka and Tangama.

Habitat and ecology

Submontane forest and edge of secondary forest. Elevation: 1070–1380 m (elevations read from Google Earth).

Conservation status

Keetia tinka is a species on current evidence endemic to the Fouta Djallon of Guinea, where it is known only from two sites, the Tinka Classified Forest, near Dalaba, and c. 30 km to the South, west of Mamou, in the Tangama Forest. Between these two sites the original submontane forest habitat is extremely fragmented to non-existent as it is throughout the Fouta Djalon, due to extensive and intensive clearance for agriculture over recent centuries:

> Submontane forest with threatened species has been all but eliminated from the `core' Fouta Djallon area that extends from Mamou, north to Dalaba....Those forest reserves that survive, such as the Tinka Classified Forest near Dalaba, have been heavily managed for forest products and appear to have lost the higher-level threatened species that they probably once possessed. Efforts to rediscover such species.....have so far failed. (Couch et al. 2019: 54).

Even though the forest canopy of the Tinka forest site is intact, Tinka forest has been heavily managed for production (and not nature conservation) and threats associated with extractive logging *activity* continue to degrade the forest habitat (Cheek and Couch pers. obs. 2016 onwards, during extensive surveys of submontane forest in the Fouta Djalon with HNG teams). The Tangama forest is much more heavily disturbed than Tinka, with fields of cultivation (noted on the specimen label), encroaching on the forest and satellite imagery indicates that about half of the area in the vicinity of the specimen collection site is cleared and lacks trees entirely (Google Earth Pro 2024). Threats to the habitat from agriculture continue. Therefore, the species is inferred to have two threat-based locations.

The area of occupancy (AOO) is 8 km² using the stipulated 2 x 2 km grid cells (IUCN 2012). The extent of occurrence (EOO) cannot be calculated from two points, so it is equated to the AOO. *Keetia tinka* can therefore be provisionally assessed as Endangered (EN) B1ab(iii)+2ab(iii) according to IUCN 2012 criteria. Further studies are needed to better understand the ecology, population and threats for this species. It is to be hoped that further sites might be found for the species. In the meantime species conservation posters for the species should be made and deployed to sensitise local communities in the vicinity of this species as to its importance. Efforts should also be made to collect seed for possible conservation, but also for immediate propagation to attempt to multiply the species at safe sites to reduce the risk of global extinction.

Notes

The two specimens of this species, *Balde* 274 and *Fofana* 303 were formerly considered for inclusion as a subspecies of *K. magassoubiana* (formerly *K. sp. aff. tenuifolia* of Bridson) until it was found that the number of mainly qualitative morphological character separating them (see Table 2) justified species rank. This conclusion is further supported by the different geographic and elevational ranges of the two taxa (Table 2). The two species also bear fruit (and so likely flower also) at different seasons.

Additional specimen examined

REPUBLIC OF GUINEA. Fouta Djalon, Dalaba Prefecture, Commune Urbaine Dalaba, pres de Yomou. Foret classee de Tangama, 10° 40’ 25.8” N 12° 15’ 49.6” W, 1328 m elev., fr., 12 July 2017, *Baldé, A.* 274 with *Couch, C., Hooper, F., Kouliye, M. & Diallo, M.* (HNG, K).

DISCUSSION

There remains an urgent need to collect flowering material for both new species so that they can be more fully characterised. It is also important to obtain much more complete populational and ecological information on these species, and to document pollination, dispersal and reproduction processes. The publication of these two new species of *Keetia* will increase the total for Guinea from the 10 *Keetia* species previously recorded (Gosline et al. 2023b), of which two are endemic, to 12 and four species respectively. This exceeds the total published for Gabon (Sosef et al. 2006) despite this being considered a far more species-diverse country. These numbers help to illustrate the unexpectedly high species diversity of Guinea and the progress now being made towards completing its inventory.

The main, most contiguous and most well-known part of the sandstone plateaus of Guinea are the Fouta Djalon that dominate Moyenne Guinee. This area is densely populated and natural habitats have been heavily impacted. Many threatened plant species recorded there a century ago have not been refound despite targeted searches (Couch et al. 2019). The discovery of a new taxon to science there (*Keetia tinka*), from recent collections, is therefore unexpected and gives hope that with further surveys, more threatened taxa might be found than are known now, even in non-pristine, secondary areas.

In contrast to the Fouta Djalon proper, the sandstone plateaux to the west, closer to the Atlantic, are less densely inhabited and probably for this reason continue to provide a flow of new species and even genera to science, despite being negatively affected primarily by grazing and artificial fires. While the southern part of this block that includes Kounounkan has seen the largest part of these discoveries, the northern part, around Kindia has also yielded discoveries, e.g. the new genus *Kindia* Cheek (Rubiaceae, Cheek et al. 2018b), and species such as *Tephrosia kindiana* Haba, B.J.Holt & Burgt (Leguminosae, Haba *et al.* 2023). These are summarized in the paper describing *Virectaria stellata* Cheek et al. (Rubiaceae, Simbiano et al. 2024).

About 75% of plant species new to science published today are already threatened (Brown et al. 2023). Usually this is because they have small ranges making them at risk of extinction from habitat clearance, making description urgent so that they can be Red Listed if this is merited, and prioritized for conservation action (Cheek et al. 2020b). Conservation actions such as improved selection and prioritization of areas for conservation (Darbyshire et al. 2017) are needed if species such as those described in this paper are not to become globally extinct as have so many other plant species (Humphreys et al. 2019;) This is especially urgent in Guinea where over 90% of original forest habitat was considered lost before the end of the 20th century (Sayer et al. 1993) and that which survives is fast being cleared. Fortunately there are positive indications that most of the area of Guinea prioritized as Important Plant Areas by Couch et al. (2019) will receive support for biodiversity protection in the near future.

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REFERENCES

Beentje H, Cheek M. 2003. Glossary. In: Beentje H. (Ed.), Flora of Tropical East Africa. Balkema, Lisse.

Breteler FJ, Baldé A. 2024. *Casearia septandra* (Salicaceae), a new tree species from the mountains of Guinea, West Africa. Kew Bulletin. 79(2): 341-344. https://doi.org/10.1007/s12225-024-10166-8

Bridson DM. 1985. The reinstatement of *Psydrax* (Rubiaceae, subfam. Cinchonoideae tribe Vanguerieae) and a revision of the African species. Kew Bulletin. 40: 687–725. https://doi.org/10.2307/4109853

Bridson DM. 1986. The Reinstatement of the African genus *Keetia* (Rubiaceae, Cinchonoideae, Vanguerieae). Kew Bulletin. 41(4): 956–994. https://doi.org/10.2307/4102996

Bridson DM. 1994. A new species of *Keetia* (Rubiaceae-Vanguerieae) Kew Bulletin. 49: 803–807. https://doi.org/10.2307/4118075

Bridson DM. 1998. Rubiaceae (Tribe Vanguerieae) Flora Zambesiaca. 5(2): 1–377. https://doi.org/10.2307/4111186

Bridson DM, Robbrecht E. 1993. A spiny-fruited new *Keetia* (Rubiaceae, Vanguerieae) from Kivu (Zaire). Belgium Journal Botany. 126: 29–32.

Bridson DM, Verdcourt B. 1991. Flora of Tropical East Africa–Rubiaceae, 3. Rotterdam/Brookfield, A.A.Balkema. https://doi.org/10.1201/9780203755860

Brown M, Bachman S, Lughadha EN. 2023. Three in four undescribed plant species are threatened with extinction. New Phytologist. 240: 1340-1344. https://doi.org/10.1111/nph.19214

Burgt van der XM, Haba PM, Magassouba S, Veranso-Libalah MC. 2022. *Benna alternifolia* (Melastomataceae: Sonerileae), a new herbaceous genus and species from Guinea, West Africa. Willdenowia. 52(1): 25–37.

Burgt XM van der, Konomou G, Haba PM, Magassouba S. 2019. *Gladiolus mariae* (*Iridaceae*), a new species from fire-free shrubland in the Kounounkan Massif, Guinea. Willdenowia. 49: 117–126. https://doi.org/10.3372/wi.49.49112

Cheek M. 2006. A New Species of *Keetia* (Rubiaceae-Vanguerieae) from Western Cameroon. Kew Bulletin. 61(4): 591–594.

Cheek M, Bridson DM. 2019. Three new threatened *Keetia* species (Rubiaceae), from the forests of the Eastern Arc Mts, Tanzania. Gardens' Bulletin Singapore. 71(Suppl.2): 155–169. https://doi.org/10.26492/gbs71(suppl.2).2019-12

Cheek M, Cable S. 1997. Plant Inventory for conservation management: the Kew-Earthwatch programme in Western Cameroon, 1993–96: 29–38. In Doolan S. (Ed.) African Rainforests and the Conservation of Biodiversity, Earthwatch Europe, Oxford.

Cheek M, Onana JM. 2024. *Keetia nodulosa* sp. nov. (Rubiaceae-Vanguerieae) of West- Central Africa: bacterial leaf nodulation discovered in a fourth genus and tribe of Rubiaceae. Webbia. 79(1): 31–46. https://doi.org/10.36253/jopt-15946

Cheek M, Bissiengou P, Lachenaud O. 2024a. *Keetia gordonii* sp. nov. (Rubiaceae - Vanguerieae), a new species of threatened forest liana from Gabon. Kew Bulletin. 79: 841–853. https://doi.org/10.1007/s12225-024-10219-y

Cheek M, Feika A, Lebbie A, Goyder D, Tchiengue B, Sene O, Tchouto P, van der Burgt X. 2017. A synoptic revision of *Inversodicraea* (Podostemaceae). Blumea. 62: 125–156. https://doi.org/10.3767/blumea.2017.62.02.07

Cheek M, Haba PK, Cisse S. 2020a. *Hibiscus fabiana* sp. nov. (Malvaceae) from the Guinea Highlands (West Africa). Blumea. 65(1): 69–74. https://doi.org/10.3767/blumea.2020.65.01.08

Cheek M, Haba PM, Konomou G & van der Burgt XM. 2019. *Ternstroemia guineensis* (Ternstroemiaceae), a new endangered, submontane shrub with neotropical affinities, from Kounounkan, Guinea, W. Africa. Willdenowia. 49 (3): 351–360. https://doi.org/10.3372/wi.49.49306

Cheek M, Harvey YB, Onana J-M. 2011. The Plants of Mefou Proposed National Park. Yaoundé, Cameroon: A Conservation Checklist. Royal Botanic Gardens, Kew.

Cheek M, Magassouba S, Howes MR, Doré T, Doumbouya, Molmou D, Grall A, Couch C, Larridon I. 2018b. *Kindia* (Pavetteae, Rubiaceae), a new cliff-dwelling genus with chemically profiled colleter exudate from Mt Gangan, Republic of Guinea. PeerJ. 6:e4666 https://doi.org/10.7717/peerj.4666

Cheek M, Magassouba S, Molmou D, Doré TS, Couch C, Yasuda S, Gore C, Guest, A, Grall A, Larridon I, Bousquet IH, Ganatra B, Gosline G. 2018a. A key to the species of *Keetia* (Rubiaceae - Vanguerieae) in West Africa, with three new, threatened species from Guinea and Ivory Coast. Kew Bulletin. 73: 56. https://doi.org/10.1007/s12225-018-9783-0

Cheek M, Molmou D, Gosline G, & Magassouba S. 2024c. *Keita* (Aptandraceae-Olacaceae sl), a new genus for African species previously ascribed to *Anacolosa*, including *K. deniseae* sp. nov., an Endangered submontane forest liana from Simandou, Republic of Guinea. Kew Bulletin 79: 317-332. https://doi.org/10.1007/s12225-024-10172-w

Cheek M, Molmou D, Magassouba S, Ghogue J-P. 2022. Taxonomic Monograph of *Saxicolella* (Podostemaceae), African waterfall plants highly threatened by Hydro-Electric projects, with five new species. Kew Bulletin 77: 403-433. https://doi.org/10.1007/s12225-022-10019-2

Cheek M, Nic Lughadha E, Kirk P, Lindon H, Carretero J, Looney B, Douglas B, Haelewaters D, Gaya E, Llewellyn T, Ainsworth M, Gafforov Y, Hyde K, Crous P, Hughes M, Walker BE, Forzza RC, Wong KM, Niskanen T. 2020b. New scientific discoveries: plants and fungi. Plants, People Planet. 2: 371–388. https://doi.org/10.1002/ppp3.10148

Cheek M, Pollard BJ, Darbyshire I, Onana JM, Wild C. 2004. The Plants of Kupe, Mwanenguba and the Bakossi Mts, Cameroon. A Conservation Checklist. Royal Botanic Gardens, Kew.

Cheek M, Poundje M, Pearce L. 2024b. *Keetia korupensis sp. nov*. (Rubiaceae - Vanguerieae) a threatened lowland evergreen forest climber and the endemic plant species of Korup National Park, SW Region, Cameroon. bioRxiv https://doi.org/10.1101/2024.06.13.598689

Cheek M, Tchiengue B, Thiam A, Molmou D, Dore TS, Magassouba S. 2024d. New discoveries of plants from Republic of Guinea, W. Africa, including *Gymnosiphon fonensis* Cheek, sp. nov. (Burmanniaceae), a new Critically Endangered species from Simandou. Adansonia. 46 (10): 89-101. https://doi.org/10.5252/adansonia2024v46a10. http://adansonia.com/46/10

Cheek M, Yasuda S, Jongkind CCH, Bowden-Pickstock J. 2025. *Keetia magassoubiana* sp. nov. (Rubiaceae - Vanguerieae), a threatened evergreen forest climber and an updated key to *Keetia* in West Africa. Kew Bulletin. 80: 141–152. https://doi.org/10.1007/s12225-024-10234-z

Couch C, Cheek M, Haba PM, Molmou D, Williams J, Magassouba S, Doumbouya S, Diallo MY. 2019. Threatened habitats and tropical important plant areas (TIPAs) of Guinea, West Africa. Kew: Royal Botanic Gardens, Kew.

Couch C, Molmou D, Magassouba S, Doumbouya S, Diawara M, Diallo MY, Keita SM, Koné F, Diallo MC, Kourouma S, Diallo MB. 2022. Piloting development of species conservation action plans in Guinea. Oryx 57(4): 497-506 (July 2023). https://doi.org/10.1017/s0030605322000138

Darbyshire I, Anderson S, Asatryan A, Byfield A, Cheek M, Clubbe C, Ghrabi Z, Harris T, Heatubun CD, Kalema J, Magassouba S, McCarthy B, Milliken W, Montmollin B de, Nic Lughadha E, Onana JM, Saıdou D, Sarbu A, Shrestha K, Radford EA. 2017. Important Plant Areas: revised selection criteria for a global approach to plant conservation. Biodiversity Conservation. 26: 1767–1800. https://doi.org/10.1007/s10531-017-1336-6

Darbyshire I, Kordofani M, Farag I, Candiga R, Pickering H. 2015. The Plants of Sudan and South Sudan. Royal Botanic Gardens, Kew.

Davies NMJ, Drinkell C, Utteridge TMA. 2023. The Herbarium Handbook. Kew Publishing

Gosline G, Bidault E, Burgt XM van der, et al. 2023a. A Taxonomically-verified and Vouchered Checklist of the Vascular Plants of the Republic of Guinea. Scientific Data. 10: 327. https://doi.org/10.1038/s41597-023-02236-6

Gosline G, Bidault E, Burgt XM van der, et al. 2023b. Checklist of the Vascular Plants of the Republic of Guinea–printable format (1.10). Zenodo. https://doi.org/10.5281/zenodo.7734985

Haba PM, Holt BJ, van der Burgt XM. 2023. *Tephrosia kindiana* (Leguminosae: Papilionoideae), a new species from Guinea. Kew Bulletin. 78; 271–276. https://doi.org/10.1007/s12225-023-10096-x

Hoekstra PH, Wieringa JJ, Maas PJM, Chatrou LW. 2021. Revision of the African species of *Monanthotaxis* (Annonaceae). Blumea. 66(2): 107–221. https://doi.org/10.1007/s12225-022-10019-2

Humphreys AM, Govaerts R, Ficinski SZ, Lughadha EN, Vorontsova MS. 2019. Global dataset shows geography and life form predict modern plant extinction and rediscovery. Nature Ecology & Evolution. 3(7): 1043–1047. https://doi.org/10.1038/s41559-019-0906-2

IPNI. 2024. International Plant Names Index. Published on the Internet http://www.ipni.org, The Royal Botanic Gardens, Kew, Harvard University Herbaria & Libraries and Australian National Herbarium. [Retrieved 16 April 2024].

IUCN. 2012. IUCN Red List Categories and Criteria: Version 3.1. Second edition.–Gland, Switzerland and Cambridge, UK: IUCN. Available from: http://www.iucnredlist.org/

Jongkind CH. 2021. *Tarenna harleyae* (Rubiaceae), a new forest species from West Africa. Phytotaxa. 520(2): 15 Sept. 2021 https://doi.org/10.11646/phytotaxa.520.2.8

Jongkind CH, Lachenaud O. 2022. Novelties in African Apocynaceae. Candollea. 77(1): 17–51. https://doi.org/10.15553/c2022v771a3

Jongkind CH. 2002. Two New Species of *Keetia* (Rubiaceae) from West Africa. Kew Bulletin. 57(4): 989–992. https://doi.org/10.2307/4115730

Lachenaud O, Luke Q, Bytebier B. 2017. *Keetia namoyae* (Rubiaceae, Vanguerieae), a new species from eastern Democratic Republic of Congo. Candollea. 72: 23–26. https://doi.org/10.15553/c2017v721a2

Lantz H, Bremer B. 2004. Phylogeny inferred from morphology and DNA data: characterizing well-supported groups in Vanguerieae (Rubiaceae). Botanical Journal of the Linnean Society. 146: 257–283. https://doi.org/10.1111/j.1095-8339.2004.00338.x

Murphy B, Onana JM. van der Burgt XM, Tchatchouang Ngansop E, Williams J, Tchiengué B, Cheek M. 2023. Important Plant Areas of Cameroon. Royal Botanic Gardens, Kew.

Onana J-M. 2011. The Vascular Plants of Cameroon. A Taxonomic Checklist with IUCN Assessments. Flore Du Cameroun 39. Ministry of Scientific Research and Innovation, Yaoundé, Cameroon.

Onana JM, Cheek M. 2011. Red Data Book of the Flowering Plants of Cameroon, IUCN Global Assessments. Royal Botanic Gardens, Kew.

POWO continuously updated. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. http://www.plantsoftheworldonline.org (downloaded 1 May. 2024).

Sayer AJ, Harcourt CZ, Collins NM. 1993. The conservation atlas of tropical forests-Africa. Journal of Tropical Ecology. 9*:* 543-543.

Simbiano FJ, van der Burgt XM, Darbyshire I, Haba PM, Konomou G, Cheek M, Couch C, Magassouba S. 2024. Possible horizontal gene transfer: *Virectaria stellata* (Sabiceeae-Rubiaceae), a new sandstone cliff species from the Republic of Guinea with stellate hairs recorded for the first time in the Rubiaceae. Webbia. 79(2): 227–237. https://doi.org/10.36253/jopt-16523

Sosef MSM, Wieringa JJ, Jongkind CCH, Achoundong G, Azizet Issembé Y, Bedigian D, Van Den Berg RG, Breteler FJ, Cheek M, Degreef J. 2006. Check-list des plantes vasculaires du Gabon. Scripta Botanica Belgica 35: 1-435. National Botanic Garden of Belgium.

Thiers BM. updated continuously. Index Herbariorum. https://sweetgum.nybg.org/science/ih/

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber W-H, Li D-Z, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF. (Eds.) 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Glashütten: Koeltz Botanical Books.

Xanthos M, Konomou G, Haba P, van der Burgt XM. 2020. *Trichanthecium tenerium* (Poaceae: Panicoideae), a new species from Guinea-Conakry. Kew Bulletin. 75: 1–7. https://doi.org/10.1007/s12225-020-9864-8

Xanthos M, Konomou G, Haba PM & van der Burgt XM. 2021. *Ctenium bennae* (Poaceae; Chloridoideae), a new rheophytic species from Guinea-Conakry. Kew Bulletin. 76: 745–750. https://doi.org/10.1007/s12225-021-09989-6

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A phylogeny of the Cotteinae (Poaceae, Chloridoideae, Eragrostideae)

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Abstract. To investigate the evolutionary relationships among 23 species in the Cotteinae we generated a DNA sequence-derived phylogeny utilizing three plastid (*rps16-trnK* spacer, *rps16* intron, *rpl32-trnL* spacer) regions and the nuclear ribosomal internal transcribed spacer (ITS) region. The Bayesian tree provides strong support for the monophyly of the Cotteinae and its four genera, in order of divergence: *Cottea*, the *Kaokochloa* + *Schmidtia* clade, and the *Enneapogon* clade. Since the Eragrostideae clearly evolved from African ancestors and *Kaokochloa*, *Schmidtia,* and *Enneapogon* all share species from Africa, we hypothesize the ancestral area of Cotteinae to be Africa. Within *Enneapogon* we recovered four major clades, the first two splits with species primarily from Africa and the third split containing a basal species from Africa/Asia/Europe sister to all species from Australia. The ancestral area of *Enneapogon* is Africa and based on our current sample the 13 species from Australia appear to be derived from a single dispersal event from an ancestor shared with *E. persicus*.

Keywords: classification, *Cottea*, *Enneapogon*, *Kaokochloa*, molecular phylogenetics, *Schmidtia.*

INTRODUCTION

The entanglement of *Enneapogon* Desv. ex P.Beauv. with *Pappophorum* Schreb. has existed for a long time and a good summary clarifying the early formulation of concepts was given in Burbidge (1941). Desvaux in Palisot de Beauvois (1812) first transferred four species to *Enneapogon*, formally placed in *Pappophorum,* and added one additional species, *E. desvauxii* P. Beauv.

Kunth (1929) reduced *Enneapogon* to a subgenus of *Pappophroum* in the tribe Pappophoreae Kunth, and then Trinius (1830) placed *Enneapogon* as a section of *Pappophorum*. Up until 1965 most agrostologists followed Desvaux in recognizing *Enneapogon* as a distinct genus within the Pappophoreae.

The subtribe Cotteinae Reeder was erected to emphasize morphological features (principally glumes and lemmas with many veins with some of the veins extending into awns, embryonic leaf having overlapping margins, dumbbell-shaped siliceous cells, and bicellular microhairs with a slender usually much elongated basal cell) to separate species of *Cottea* Kunth, *Enneapogon*, *Kaokochloa* DeWinter, and *Schmidtia* Steud. ex J.A.Schmidt from *Pappophorum* (Reeder 1965). Whereas *Pappophorum* (subtr. Pappophorinae) includes species with single-veined glumes and lemmas with veins extending into awns, embryonic leaf with margins that meet but do not overlap, saddle- or double axe-shaped siliceous cells, and short-stalked eragrostoid-type bicellular microhairs (Reeder 1965; Reeder 2003). Historically, most grass classifications included these genera in the Pappophoreae (Stebbins and Crampton 1961; Clayton 1970; Peterson et al. 2001; Weiller and Lazarides 2005; Roodt-Wilding and Spies 2006; Cope 2007), although Clayton and Renvoize (1986) placed the Cotteinae as a synonym of the Pappophoreae, and it was not until molecular DNA sequence studies emerged that our modern concept of the Pappophorinae was formed, consisting of *Neesiochloa* Pilg., *Pappophorum*, and *Tridens* Roem. & Schult. s.s. realigned in the tribe Cynodonteae Dumort. (Peterson et al. 2010a; Reutemann et al. 2011; Peterson et al. 2016; Soreng et al. 2015, 2017, 2022). The subtribes Cotteinae, Eragrostidinae J. Presl (*Eragrostis* Wolf), and Uniolinae Clayton (*Entoplocamia* Stapf, *Fingerhuthia* Nees ex Lehm., *Tetrachne* Nees, and *Uniola* L.) are all members of the tribe Eragrostideae Stapf (Peterson et al. 2010a; Soreng et al. 2022).

Within the Cotteinae, *Enneapogon* is the largest genus with at least 26 species, one cosmopolitan (*E. desvauxii*, although not found in Australia), 15 are endemic to Australia, six are found in southern Africa, and at least six extend into Asia (Phillips 1995; Weiller and Lazarides 2005; Cope 2007; Fish et al. 2015; Clayton et al. 2016; Plants of the World Online 2025). *Schmidtia* with two species is found in Africa and Pakistan, *Kaokochloa* with a single species occurs in southern Africa and northwestern Namibia, and *Cottea* with a single species is found in North and South America (Phillips 1995; Cope 2007; Fish et al. 2015). The genera of the Cotteinae can be differentiated by their lemma shape and the number of awns emanating from the apex. *Cottea* and *Schmidtia* have lobed lemmas (irregularly so in *Cottea*) with the former having 7–11 awns and the latter having only five awns, whereas *Enneapogon* and *Kaokochloa* have unlobed lemmas with the former having nine awns and the latter having two lateral awns with one or two additional central awns (never more than four awns total) [Renvoize 1988; Phillips 1995; Cope 2007; Fish et al. 2015; Clayton et al. 2016]. The spikelets of *Cottea* also disarticulate above the glumes and between the florets while all other members of the subtribe have spikelets that disarticulate above the glumes but not between the florets (Reeder 2003).

In a recent nuclear and plastid DNA-derived phylogeny of the entire grass family the Cotteinae is sister to remaining members of the Eragrostideae, and the Cotteinae has the following structure: (Cottea (*Kaokochloa* + *Schmidtia*) *Enneapogon*)) [Group Phylogeny Working Group (GPWG) 2024]. Another previous DNA-derived phylogeny indicated that *Schmidtia* was paraphyletic with species of *Enneapogon* forming a monophyletic clade nested within *Schmidtia* (based on ITS) or included in a polytomy (based on the plastid *trnL-F* marker) [Reutemann et al. 2011]. In our study we provide the latest estimate of the phylogeny within the Cotteinae by analyzing three markers from the plastid genome (*rps16-trnK* spacer, *rps16* intron, *rpl32-trnL* spacer) and one from the nuclear genome (ITS). In comparison with the Reutemann et al. (2011) and GPWG (2024) studies we increase the sample size of *Enneapogon* from four (nuclear) and five samples (plastid) to 19 species.

MATERIAL AND METHODS

Taxon sampling

We sampled 64 individuals, representing 50 total species, and 19 (19/26 = 73%) species of *Enneapogon*, two (2/2 = 100%) species of *Schmidtia*, one species (1/1 = 100%) of *Cottea*, and one (1/1 = 100%) species of *Kaokochloa*. A complete list of taxa including authorities, voucher information, and GenBank numbers is presented in Appendix 1. A few of these DNA sequences were previously published in GenBank. We submitted 128 new sequences to GenBank, 102 of these representing *Enneapogon*, 16 in *Schmidtia*, eight in *Fingerhuthia,* and two in *Kaokochloa*.

We designed our study to characterize relationships among species of Cotteinae (*Cottea*, *Enneapogon*, *Kaokochloa,* and *Schmidtia*) and including outgroups from the Eragrostidinae J.Presl [*Eragrostis conrathii* (Hack.) S.M.Phillips, *E. dielsii* Pilg., *E. tincta* S.M.Phillips, and *E. xerophila* Domin]; Uniolinae [*Entoplocamia aristulata* (Hack. & Rendle) Stapf, *Fingerhuthia africana* Nees es Lehm., *F. sesleriiformis* Nees, *Tetrachne dregei* Nees, and *Uniola paniculata* L.]; Cynodonteae Dumort. [*Chloris barbata* Sw., *Cynodon plectostachyus* (K. Schum.) Pilg., *Eleusine indica* (L.) Gaertn., *Gymnopogon grandiflorus* Roseng., B.R.Arill. & Izag., *Halopyrum mucronatum* (L.) Stapf, *Leptothrium rigidum* Kunth, *Oropetium capense* Stapf, *Pappophorum bicolor* E.Fourn., *P. casepitosum* R.E.Fr., *P. pappiferum* (Lam.) Kuntze*, P. philippianum* Parodi, *P.*

vaginatum Buckley, and *Tripogon chinensis* Hack.]; and Zoysieae Benth. [*Sporobolus pyramidatus* (Lam.) Hitchc., *S. virginicus* (L.) Kunth, and *Zoysia macrantha* Desv.]; and Triraphideae P.M.Peterson (*Triraphis mollis* R.Br. and *T. ramosissima* Hack.) [Soreng et al. 2022].

Phylogenetic methods

All procedures related to the sequencing of the plastid and ITS regions were performed in the Laboratory of Analytical Biology at the Smithsonian Institution. Detailed methods for DNA extraction, amplification, and sequencing are given in Romaschenko et al. (2012) and Peterson et al. (2010a, 2010b, 2012, 2014, 2015a, 2015b, 2016). Geneious Prime v.2020.1.4 (Kearse et al. 2012) was utilized for contig assembly of bidirectional sequences of *rps16-trnK* spacer, *rps16* intron, *rpl32-trnL* spacer, and ITS regions; and Muscle (Edgar 2004) to align consensus sequences and adjust the final alignment. The Bayesian trees were constructed with MrBayes v3.2.7 (Huelsenbeck and Ronquist 2001; Ronquist et al. 2012).

The evolutionary model parameters for each region were estimated with GARLI 2.0 (Zwickl, 2006) (Table 1) and used as priors in Bayesian analysis. The combined data set was split into four partitions containing the ITS, *rpL32-trnL*, *rps16-trnK*, and *rps16* intron sequences. Bayesian analysis was initiated with random starting trees and was run for four million generations with every 1000th iteration being sampled. Upon completion of the search, the variance of split sequences was less than 0.01 and the potential scale reduction factor was close or equal to 1.0 indicating convergence of the chains (Huelsenbeck and Ronquist 2001). The search was monitored with Tracer v1.7.1 (Rambaut et al. 2018). The effective sample size (ESS) value was greater than 100, and 25% of the sampled values were discarded. All compatible branches were saved. Posterior probabilities (PP) of ≥0.95 indicated a credible interval of probability.

The parsimony bootstrap analysis (Felsenstein 1985) was performed using program IQ-Tree 3.0.1 implementing ultrafast bootstrap approximation (with 10000 bootstrap replicates) to assess branch supports (Minh et al. 2013; Hoang et al. 2018). Bootstrap values (BS) of ≥95% were interpreted as strong support.

RESULTS

Phylogenetic analyses

One hundred twenty-eight sequences (128/246 = 52%) in our study are newly reported in GenBank and 44% (108/246) are previously published sequences (Appendix 1)

Table 1. Characteristics of the four regions, *rps16-trnK, rps16* intron*, rpL32-trnL*, ITS, and parameters used in phylogenetic analysis, indicated by Akaike Information Criterion (AIC).

	rps16-trnK	*rps16 intron*	*rpL32-trnL*	Combined plastid data	*ITS*	Overall
Total aligned characters	1020	1019	1062	3101	745	3846
Number of sequences (success)	61 (95.3%)	60 (93.8 %)	63 (98.4%)	184 (95.8%)	62 (96.9%)	246 (96.1%)
Number of new sequences (ratio)	32 (52.5%)	31 (51.7%)	33 (52.4%)	96 (52.2%)	32 (51.6%)	128 (52.0%)
Likelihood score (-lnL)	3303.89	2907.35	3186.56		7719.76	
Number of substitution types	4	4	4	-	4	-
Model for among-sites rate variation	gamma	gamma	gamma	-	Invar+Gamma	-
Substitution rates	2.0469 4.1996 1.0000 2.0469 4.1996 1.0000	1.0000 1.5457 0.4216 0.4216 1.5457 1.0000	1.9637 2.6823 1.0000 1.9637 2.6823 1.0000	-	0.9023 2.1809 1.8644 0.4373 4.4558 1.0000	-
Character state frequencies	0.2893 0.1526 0.1585 0.3995	0.3757 0.1334 0.1855 0.3054	0.3438 0.1487 0.1430 0.3645	-	0.2170 0.2948 0.2867 0.2016	-
Proportion of invariable sites	0.7695	0.8365	0.6556	-	0.3163	-
Substitution model	TPM3u+F+G4	K3Pu+F+G4	TPM3u+F+G4	-	GTR+F+I+G4	-
Gamma shape parameter (α)	0.8768	0.4794	0.6840	-	1.3470	-

generated for earlier studies (Peterson et al. 2010a; 2015a; 2016), and two individuals: *Enneapogon desvauxii* and *E. oblongus* N.T.Burb. were available from GenBank. Four percent (10/256) of the sequences (ITS and plastid) in our dataset are missing. Total aligned characters for individual regions and other parameters are shown in Table 1.

Phylogeny

The Bayesian tree based on plastid (*rps16-trnK* spacer, *rps16* intron, *rpl32-trnL* spacer) and ITS regions is well resolved and a monophyletic Cotteinae including *Cottea, Enneapogon, Kaokochloa*, and *Schmidtia* is strongly supported (BS = 95–100; PP = 0.95–1.00) [Fig. 1]. The first split within the Cotteinae is *Cottea pappophoroides* Kunth and the second split includes *Kaokochloa nigrirostris* De Winter sister to three accessions of *Schmidtia pappophoroides* Steud. ex J.A.Schmidt + two accessions of *S. kalaharensis* Stent. The second split (*Kaokochloa nigrirostris* (*Schmidtia pappophoroides* + *S. kalaharensis*)) is then sister to a monophyletic clade containing 19 species of *Enneapogon*. The *Enneapogon* clade's first split is (*E. pretoriensis* Stent + *E. scaber* Lehm.) sister to remaining species in the genus. The second split in the *Enneapogon* clade contains two major clades: (*Enneapogon scoparius* Stapf + four accessions of *E. cenchroides* (Licht. ex Roem. & Schult.) C.E.Hubb.) *E. desvauxii*); and *Enneapogon persicus* Boiss. (*E. nigricans* (R.Br.) P.Beauv. (*E. pallidus* (R.Br.) P.Beauv. (two accessions of *E. eremophilus* Kakudidi)) + *E. purpurascens* (R.Br.) P.Beauv. (*E. cylindricus* N.T.Burb. (two accessions of *E. avenaceus* (Lindl.) C.E.Hubb.)); sister to (two accessions of *E. polyphyllus* (Domin) N.T.Burb.+ two accessions of *E. intermedius* N.T.Burb.) + (*E. robustissimus* (Domin) N.T.Burb.+ *E. oblongus*) + (*E. lindleyanaus* (Domin) C.E.Hubb. (*E. caerulescens* (Gaudich.) N.T.Burb.+ *E. gracilis* (R.Br.) P.Beauv.)).

DISCUSSION

Phylogeny

The combined plastid/nuclear DNA-derived phylogeny supports three strongly supported monophyletic clades containing the Cotteinae, *Kaokochloa-Schmidtia*, and *Enneapogon*. *Schmidtia* was earlier found to be paraphyletic often aligning within the *Enneapogon* clade (Roodt-Wilding et al. 2006; Reutemann et al. 2011). We compared our ITS sequences (KM010328, PV954974, PV954975) of *Schmidtia papporphoroides* with the sequence used in Reutemann et al. (2011) and

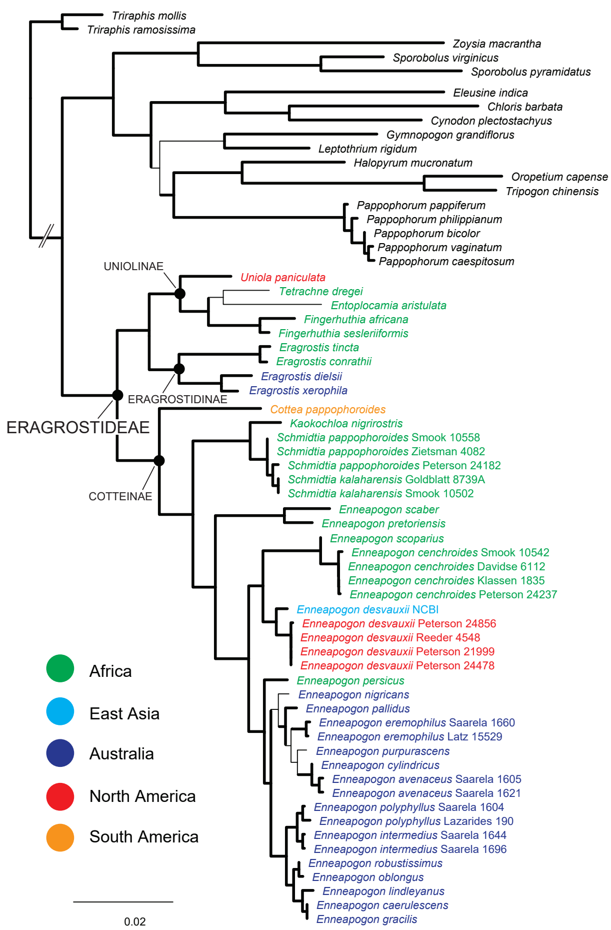

Figure 1. Bayesian tree inferred from combined plastid (*rps16-trnK, rps16, rpl32-trnL*) and nuclear (ITS) DNA sequences of the Cotteinae. Thick black branches in the phylogram indicate a bootstrap of 95–100 and/or posterior probability of 0.95–1.00. Scale bar = 2% substitutions per site.

Roodt-Wilding and Spies (2006) available in GenBank (DQ65584). The latter sequence was poorly edited with 57 possibly erroneous nucleotide substitutions. However, we did not use the plastid *trnL-F* marker in our analysis which also led to equivocal placement of *Schmidtia papporphoroides* in their analysis.

Burbidge (1941) indicated that the Australian species of *Enneapogon* separated into two groups, those with ribbed or prominently thickened nerves (veins) on the lemmas [*E. nigricans* = *E. flavescens* (Lindl.) N.T.Burb.], and those with a smooth lemmas, i.e., the veins not prominent (*E. avenaceus*). Our phylogeny (Fig. 1) does not support this hypothesis, at least in a phylogenetic context, since species with a smooth lemma are not always united in a subclade within the Australian *Enneapogon* clade. However, two accessions each of *Enneapo-*

gon intermedius and *E. polyphyllus* are sister in a subclade but *E. caerulescens, E. lindleyanus, E. oblongus,* and *E. robustissimus*, all treated by Burbidge (1941) as having prominently thickened veins are found in a clade with *E. gracilis* (treated as having smooth lemmas), whereas two accessions of *E. avenaceus* are sister to *E. cylindricus* (treated as having prominently thickened veins) in a different subclade. Burbidge does indicate that the ribbed lemma is probably a more primitive form found in species outside of Australia. Our Australian clade is sister to *E. persicus*, a species from the middle east, Asia, Africa, Spain, and India (Bor 1960, 1970; Chen and Phillips 2006; Cope 2007; Clayton et al. 2016; Aedo 2021; POWO 2025). *Enneapogon persicus* has ribbed lemmas and the first two splits within the genus are composed of primarily African species all with ribbed lemmas.

Biogeography

The tribe Eragrostideae clearly evolved from African ancestors since the stem (42.75 Ma) and crown (31.15 Ma) ages indicate the ancestral area to be Afrotropical 73% and 43%, respectively (Gallaher et al. 2022). The Cotteinae and Unioliinae each have a basal genus, *Cottea* and *Uniola,* that includes species with a western hemisphere distribution. Therefore, it is extremely hard to determine what the ancestral area for each of these subtribes might be. *Cottea pappophoroides* occurs in southwestern United States to central, eastern, and southern Mexico, and again in South America from Ecuador, Peru, Bolivia, and Argentina (Peterson et al. 2001; Sanchez-Ken 2018; Davila et al. 2019). Gallaher et al. (2022) determined the ancestral area for Cotteinae to be 10% cosmopolitan (from anywhere). However, based on our study the most plausible ancestral area for Cotteinae is African since *Kaokochloa* and *Schmidtia* are from Africa, and the first split of *Enneapogon* (*E. pretoriensis* and *E. scaber*), includes species distributed in Africa (Fish et al. 2015). We hypothesize that early in the evolutionary history of Cotteinae, individuals of proto-*Cottea* dispersed to the western hemisphere.

Within *Enneapogon* we recovered four major clades, the first two splits with species primarily from Africa and the third split containing a basal species from Africa/Asia/Europe (*E. persicus*) sister to all species from Australia (Bor 1960, 1970; Chen and Phillips 2006; Cope 2007; Clayton et al. 2016; Aedo 2021; POWO 2025). The ancestral area of *Enneapogon* is Africa since it shares a common ancestor with the *Kaokochloa*-*Schmidtia* clade and based on our current sample the 13 species from Australia appear to be derived from a single dispersal event from an ancestor shared with *E. persicus*.

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REFERENCES

Aedo C. 2021. 121. *Enneapogon* Desv. ex P.Beauv. In: Romero Zarco C, Rico E, Crespo MB, Devesa JA, Buira A, Aedo C (Eds.), Flora Iberica Plantas vasculares de la Península Ibérica e Islas Baleares Vol. XIX(II) Gramineae (partim). Real Jardín Botánico, CSIC, Madrid, 1310-1312.

Bor NL. 1960. The grasses of Burma, Ceylon, India, and Pakistan (excluding Bambuseae). Pergamon Press, Oxford, 1-767.

Bor NL. 1970 Gramineae. In: Rechinger KH (Ed.), Flora Iranica 70/30. Akademische Druck und Verlagsanstalt, Graz, Austria, 1–573.

Burbidge NT. 1941. A revision of the Australian species of *Enneapogon* Desv. Proceedings of the Linnean Society of London. 153(1): 52-91.

Chen SL, Phillips SM. 2006. 21. Tribe Pappophoreae. In: Wu ZY, Raven PH, Hong DY (Eds.), Flora of China: Poaceae, volume 22. Science Press, Beijing and Missouri Botanical Garden Press, St. Louis, 456–457.

Clayton WD. 1970. Gramineae (Part 1). In: Milne-Redhead E, Polhill RM (Eds.), Flora of Tropical East Africa. Whitefriars Press, London, 1-176.

Clayton WD, Renvoize SA. 1986. Genera graminum: Grasses of the World. Kew Bulletin, Additional Series. 13: 1–389.

Clayton WD, Vorontsova MS, Harman KT, Williamson H. 2016. GrassBase — The online World grass flora: The Board of Trustees, Royal Botanic Gardens. http://www.kew.org/data/grasses-db.html (accessed 29 July 2025).

Cope, TA. 2007. Poaceae (Gramineae) In: Knees SG, Miller AG (Eds.), Flora of the Arabian Peninsula and Socotra, vol. 5 part 1. Edinburgh University Press and Royal Botanic Gardens, Kew. Edinburgh, 1-387.

Dávila P, Mejia-Saulés MT, Soriano-Martínez AM, Herrera-Arrieta Y. 2018. Conocimiento taxonómico de la Poaceae en México. Botanical Sciences. 96(3): 462–514. https://doi.org/10.17129/botsci.1894

Edgar R. 2004. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research. 32: 1792–1797.

Felsenstein J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution. 39: 783–791.

Fish L, Mashau AC, Moeaha MJ, Nembudani MT. 2015. Identification guide to Southern African grasses, an identification manual with keys, descriptions and distributions. Strelitzia. 36(ix): 1–798.

Gallaher TJ, Peterson PM, Soreng RJ, Zuloaga FO, Li DZ, Clark LG, Tyrrell CD, Welker CAD, Kellogg EA, Teisher JK. 2022. Grasses through space and time: An overview of the biogeographical and macroevolutionary history of the Poaceae. Journal of Systematics and Evolution. 60(3): 522-569. https://doi.org/10.1111/jse.12857

Grass Phylogeny Working Group (GPWG) III Arthan W +72 additional authors, 2024. A nuclear phylogenomic tree of grasses (Poaceae) recovers current classification despite gene tree incongruence. New Phytologist. 245(2) 818-834. https://doi.org/10.1111/nph.20263

Hoang DT, Chernomor O, von Haeseler A, Minh BQ, Vinh LS. 2018. UFBoot2: Improving the ultrafast bootstrap approximation. Molecular Biology and Evolution. 35(2): 518-522. https://doi.org/10.1093/molbev/msx281

Huelsenbeck JP, Ronquist FR. 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics (Oxford, England). 17(8): 754–755.

Kunth KS. 1929. Révision des Graminées, Vol. 1. Dessins de Madame Eulalia Delile, Paris.

Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P, Drummond A. 2012. Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics. 28: 1647–1649. https://pmc.ncbi.nlm.nih.gov/articles/PMC3371832/

Minh BQ, Nguyen MAT, von Haeseler A. 2013. Ultrafast approximation for phylogenetic bootstrap. Molecular Biology and Evolution. 305: 1188-1195. https://doi.org/10.1093/molbev/mst024

Palisot de Beauvois AMFJ. 1812. Essai d'une nouvelle agrostographie; ou nouveaux genres des Graminées; avec figures représentant les caractères de tous les genres. Fain, Paris, France, 1-82.

Peterson PM, Romaschenko K, Herrera Arrieta Y. 2015a). A molecular phylogeny and classification of the Eleusininae with a new genus, *Micrachne* (Poaceae: Chloridoideae: Cynodonteae). Taxon. 64(3): 445–467. https://doi.org/10.12705/643.5

Peterson PM, Romaschenko K, Herrera Arrieta Y. 2015b. Phylogeny and subgeneric classification of *Bouteloua* with a new species, *B. herrera-arrietae* (Poaceae: Chloridoideae: Cynodonteae: Boutelouinae). Journal of Systematics and Evolution. 53(4): 351–366. https://doi.org/10.1111/jse.12159

Peterson PM, Romaschenko K, Herrera Arrieta Y. 2016. A molecular phylogeny and classification of the Cynodonteae (Poaceae: Chloridoideae) with four new genera: *Orthacanthus*, *Triplasiella*, *Tripogonella*, and *Zaqiqah*; three new subtribes: Dactylocteniinae, Orininae, and Zaqiqahinae; and a subgeneric classification of *Distichlis*. Taxon. 65(6): 1263–1287. https://doi.org/10.12705/656.4

Peterson PM, Romaschenko K, Johnson G. 2010a. A classification of the Chloridoideae (Poaceae) based on multi-gene phylogenetic trees. Molecular Phylogenetics and Evolution. 55: 580–598. https://doi.org/10.1016/j.ympev.2010.01.018

Peterson PM, Romaschenko K, Johnson G. 2010b. A phylogeny and classification of the Muhlenbergiinae (Poaceae: Chloridoideae: Cynodonteae) based on plastid and nuclear DNA sequences. American Journal of Botany. 97: 1532–1554. https://doi.org/10.3732/ajb.0900359

Peterson PM, Romaschenko K, Soreng RJ. 2014. A laboratory guide for generating DNA barcodes in grasses: A case study of *Leptochloa* s.l. (Poaceae: Chloridoideae). Webbia. 69(1): 1–12. https://doi.org/10.1080/00837792.2014.927555

Peterson PM, Soreng RJ, Davidse G, Filgueiras TS, Zuloaga FO, Judziewicz EJ. 2001. Catalogue of New World grasses (Poaceae): II. subfamily Chloridoideae. Contributions from the United States National Herbarium 41: 1–255. https://www.biodiversitylibrary.org/item/13801#page/1/mode/1up

Phillips SM. 1995. Poaceae (Gramineae). In: Hedberg I, Edwards S (Eds.), Flora of Ethiopia and Eritrea. The National Herbarium, Addis Abada University, Addis Abada, Ethiopia and Department of Systematic Botany, Uppsala Sweden, 1–420.

Plants of the World Online (POWO). 2025. Facilitated by the Royal Botanic Gardens, Kew http://www.plantsoftheworldonline.org (accessed 29 July 2025).

Reeder JR. 1965. The tribe Orcuttieae and the subtribes of the Pappophoreae (Gramineae). Madroño. 18(1): 18-28. https://www.jstor.org/stable/41423175

Reeder JR. 2003. 18. Pappophoreae Kunth In: Barkworth ME, Capels KM, Long S, Piep MB (Eds.), Flora of North America North of Mexico, Vol. 25 Magnoliophyta: Commelinidae (in part): Poaceae, part 2. Oxford University Press, New York, 285-289.

Rambaut A, Drummond A, Xie D, Baele G, Suchard M. 2018. Posterior summarization in Bayesian phylogenetics using tracer 1.7. Systematic Biology. 67(5): 901-904. https://doi.org/10.1093/sysbio/syy032

Renvoize SA. 1968. The Afro-Asian species of *Enneapogon* P. Beauv. (Gramineae). Kew Bulletin. 22: 393–401.

Reutemann AG, Tivano JC, Lucero LE, Vegetti AC, Giussani LM. 2011. Phylogenetic relationships within Pappophoreae s.l. (Poaceae: Chloridoideae): Additional evidence based on ITS and *trnL-F* sequence data. South African Journal of Botany. 77: 693-702. https://doi.org/10.1016/j.sajb.2011.03.010

Romaschenko K, Peterson PM, Soreng RJ, Garcia-Jacas N, Futorna O, Susanna A. 2012. Systematics and evolution of the needle grasses (Poaceae: Pooideae: Stipeae) based on analysis of multiple chloroplast loci, ITS, and lemma micromorphology. Taxon. 61(1): 18–44. https://doi.org/10.1002/tax.611002

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. Systematic Biology. 61: 539–542. https://academic.oup.com/sysbio/article/61/3/539/1674894

Roodt-Wilding R, Spies JJ. 2006. Phylogenetic relationships in southern African chloridoid grasses (Poaceae) based on nuclear and chloroplast sequence data. Systematic and Biodiversity. 4(4): 401–415. https://doi.org/10.1017/S1477200006002131

Sanchez-Ken JG. 2018. Riqueza de especies, clasificación y listado de las gramíneas (Poaceae) de México. Acta Botánica Mexicana. 126(126): 1–115. https://doi.org/10.21829/abm126.2019.1379

Soreng RJ, Peterson PM, Romaschenko K, Davidse G, Zuloaga FO, Judziewicz EJ, Filgueiras TS, Davis JI, Morrone O. 2015. A worldwide phylogenetic classification of the Poaceae (Gramineae). Journal of Systematics and Evolution. 53(2): 117–137. https://onlinelibrary.wiley.com/doi/10.1111/jse.12150/epdf

Soreng RJ, Peterson PM, Romaschenko K, Davidse G, Teisher JK, Clark LG, Barberá B, Gillespie LJ, Zuloaga FO. 2017. A worldwide phylogenetic classification of the Poaceae (Gramineae) II: An update and a comparison of two 2015 classifications. Journal of Systematics and Evolution. 55(4): 259–290. https://doi.org/10.1111/jse.12262

Soreng RJ, Peterson PM, Zuloaga FO, Romaschenko K, Clark LG, Teisher JK, Gillespie LJ, Barberá P, Welker CAD, Kellogg EA, De-Zhu L, Davidse G. 2022. A worldwide phylogenetic classification of the Poaceae (Gramineae) III: An update. Journal of Systematics and Evolution. 60(3): 476–521. https://doi.org/10.1111/jse.12847

Stebbins GL, Crampton B. 1961. A suggested revision of the grass genera of temperate North America. Recent Advances in Botany: 133-145. University of Toronto Press.

Trinius CB. 1830.Graminum Genera quadam speciesque complures definitionibus novis ilustravit. Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 1(1): 54-93.

Weiller CM, Lazarides M. 2005. *Enneapogon*. In: Mallett K (Ed.), Flora of Australia Volume 44B Poaceae 3. CSIRO Publishing, Melbourne, 1-486.

Zwickl DJ. 2006. Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. University of Texas, Austin.

Appendix 1. Taxon voucher (collector, number, and where the specimen is housed), country of origin, and GenBank accession for DNA sequences of *rps16-trnK, rps16 intron, rpl32-trnL,* and ITS regions; **bold** indicates new accession; a dash (–) indicates missing data; an asterisk (*) indicates type for the genus.

	Taxa	Voucher	Country	*rps16-trnK*	*rps16 intron*	*rpl32-trnL*	ITS
1	*Chloris barbata* Sw.	Peterson 22255 & Saarela (US)	Mexico, Sinaloa	GU360514	GU360435	GU359873	GU359320
2	*Cottea pappophoroides* Kunth	Peterson 21463, Soreng, LaTorre & Rojas Fox (US)	Peru, Ancash	GU360600	GU360456	GU359842	GU359237
3	*Cynodon plectostachyus* (K.Schum.) Pilg.	Troupin 11610 (US)	Rwanda	GU360592	GU360449	GU359890	GU359247
4	*Eleusine indica* (L.) Gaertn.	Peterson 21362, Saarela & Flores Villegas (US)	Mexico, Mexico	GU360496	GU360472	GU359797	GU359338
5	*Enneapogon avenaceus* (Lindl.) C.E.Hubb.	Saarela 1605, Peterson, Soreng & Judziewicz (US)	Australia, Northern Territory	**PV982154**	**PV982186**	**PV959292**	**PV954944**
6	*Enneapogon avenaceus* (Lindl.) C.E.Hubb.	Saarela 1621, Peterson, Soreng & Judziewicz (US)	Australia, Northern Territory	**PV982155**	**PV982187**	**PV959293**	**PV954945**
7	*Enneapogon caerulescens* (Lindl.) C.E.Hubb.	Trudgen 15129 (MEL)	Australia, Western Australia	**PV982156**	**PV982188**	**PV959294**	**PV954946**
8	*Enneapogon cenchroides* (Licht. ex Roem. & Schult.) C.E.Hubb.	Davidse 6112 & Loxton (MO)	South Africa, Northern Cape	**PV982157**	**PV982189**	**PV959295**	**PV954947**
9	*Enneapogon cenchroides* (Licht. ex Roem. & Schult.) C.E.Hubb.	Klaassen 1835, Rugheimer, Mannheimer, Hochobes & Hasheela (US)	Namibia, Karas	**PV982158**	**PV982190**	**PV959296**	**PV954948**
10	*Enneapogon cenchroides* (Licht. ex Roem. & Schult.) C.E.Hubb.	Peterson 24237, Soreng, Romaschenko & Mbago (US)	Tanzania, Tanga	**PV982159**	**PV982191**	**PV959297**	**PV954949**
11	*Enneapogon cenchroides* (Licht. ex Roem. & Schult.) C.E.Hubb.	Smook 10542 (MO)	South Africa, Northern Cape	**PV982160**	**PV982192**	**PV959298**	**PV954950**
12	*Enneapogon cylindricus* N.T.Burb.	Latz 14219 (MEL)	Australia, Northern Territory	**PV982161**	**PV982193**	**PV959299**	**PV954951**
13	**Enneapogon desvauxii* P.Beauv.	GenBank (NCBI)	China	OM307675	OM307675	OM307675	MF029719
14	**Enneapogon desvauxii* P.Beauv.	Peterson 21999 & Saarela (US)	Mexico, Chihuahua	GU360495	GU360486	GU359796	GU359339
15	**Enneapogon desvauxii* P.Beauv.	Peterson 24478 & Romaschenko (US)	Mexico, Coahuila	**PV982162**	**PV982194**	**PV959300**	**PV954952**
16	**Enneapogon desvauxii* P.Beauv.	Peterson 24856 & Romaschenko (US)	Mexico, San Luis Potosí	**PV982163**	**PV982195**	**PV959301**	**PV954953**
17	**Enneapogon desvauxii* P.Beauv.	Reeder 4548 & Reeder (US)	USA, Texas	**PV982164**	**PV982196**	**PV959302**	**PV954954**
18	*Enneapogon eremophilus* Kakudidi	Saarela 1660, Peterson, Soreng & Judziewicz (US)	Australia, Northern Territory	**PV982165**	**PV982197**	**PV959303**	**PV954955**
19	*Enneapogon eremophilus* Kakudidi	Latz 15529 (MEL)	Australia, Northern Territory	**PV982166**	**PV982198**	**PV959304**	**PV954956**
20	*Enneapogon gracilis* P.Beauv.	Walsh, Stewart & O'Brien 6957 (MEL)	Australia, Victoria	**PV982167**	**PV982199**	**PV959305**	**PV954957**
21	*Enneapogon intermedius* N.T.Burb.	Saarela 1644, Peterson, Soreng & Judziewicz (US)	Australia, Northern Territory	**PV982168**	**PV982200**	**PV959306**	**PV954958**
22	*Enneapogon intermedius* N.T.Burb.	Saarela 1696, Peterson, Soreng & Judziewicz (US)	Australia, Northern Territory	**PV982169**	**PV982201**	**PV959307**	**PV954959**
23	*Enneapogon lindleyanus* (Domin) C.E.Hubb.	Jobson 1106 (MEL)	Australia, Queensland	**PV982170**	**PV982202**	**PV959308**	**PV954960**
24	*Enneapogon nigricans* (R.Br.) P.Beauv.	Hosking 2490 (MEL)	Australia, New South Wales	**PV982171**	**PV982203**	**PV959309**	**PV954961**
25	*Enneapogon oblongus* N.T.Burb.	USDA PI238297	Australia	NC036682	NC036682	NC036682	–
26	*Enneapogon pallidus* P.Beauv.	Dixon 1300 (MO)	Australia, Northern Territory	**PV982172**	**PV982204**	**PV959310**	**PV954962**
27	*Enneapogon persicus* Boiss.	Peterson 24265, Soreng, Romaschenko & Mbago (US)	Tanzania, Shinyanga	**PV982173**	**PV982205**	**PV959311**	**PV954963**
28	*Enneapogon polyphyllus* (Domin) N.T.Burb.	Lazarides 190 & Palmer (MO)	Australia, Northern Territory	**PV982174**	**PV982206**	**PV959312**	**PV954964**
29	*Enneapogon polyphyllus* (Domin) N.T.Burb.	Saarela 1604, Peterson, Soreng & Judziewicz (US)	Australia, Northern Territory	**PV982175**	**PV982207**	**PV959313**	**PV954965**
30	*Enneapogon pretoriensis* Stent	Balkwill 6765, Balkwill & Cron (MO)	South Africa, Transvaal	**PV982176**	–	**PV959314**	–
31	*Enneapogon purpurascens* P.Beauv.	Latz 13064 (MO)	Australia, Northern Territory	**PV982177**	**PV982208**	**PV959315**	**PV954966**
32	*Enneapogon robustissimus* (Domin) N.T.Burb.	Latz 12379 (US)	Australia, Northern Territory	**PV982178**	**PV982209**	**PV959316**	**PV954967**
33	*Enneapogon scaber* Lehm.	Sachse 008 (MO)	South Africa, Western Cape	JQ345237	JQ345279	JQ345322	JQ345168
34	*Enneapogon scoparius* Stapf	Smook 9055 (MO)	Namibia	**PV982179**	**PV982210**	**PV959317**	**PV954968**

(Continued)

Appendix 1. (Continued).

	Taxa	Voucher	Country	*rps16-trnK*	*rps16 intron*	*rpl32-trnL*	ITS
35	*Entoplocamia aristulata* (Hack. & Rendle) Stapf	Seydel 187 (US)	Namibia	GU360492	GU360468	GU359793	GU359342
36	*Eragrostis conrathii* (Hack.) S.M.Phillips	Schweickerdt 1652 (US)	South Africa, Pretoria	–	–	MK872569	MK863244
37	*Eragrostis dielsii* Pilg.	Peterson 14399, Soreng & Rosenberg (US)	Australia, Western Australia	GU360537	GU360400	GU359779	GU359297
38	*Eragrostis tincta* S.M.Phillips	Kemp 1290 (MO)	Swaziland	MK872800	MK872655	MK872567	MK863242
39	*Eragrostis xerophila* Domin	Saarela 1624, Peterson, Soreng & Judziewicz (US)	Australia, Northern Territory	MK872798	MK872653	MK872565	MK863240
40	**Fingerhuthia africana* Nees ex Lehm.	Bester 7070 (MO)	South Africa, Northern Cape	**PV982180**	**PV982211**	**PV959318**	**PV954969**
41	*Fingerhuthia sesleriiformis* Nees	Phillipson 608 (MO)	South Africa, Eastern Cape	**PV982181**	**PV982212**	**PV959319**	**PV954970**
42	*Gymnopogon grandiflorus* Roseng., B.R.Arill. & Izag.	Peterson 16642 & Refulio-Rodriguez (US)	Peru, Apurimac	GU360581	GU360383	GU359816	GU359200
43	**Halopyrum mucronatum* (L.) Stapf	Peterson 23837, Soreng, Romaschenko & Abeid (US)	Tanzania, Lindi	KX582970	KX582903	KX582650	KX582374
44	**Kaokochloa nigrirostris* De Winter	Smook 7779 (MO)	Namibia, Kaokoveld	–	–	**PV959320**	**PV954971**
45	**Leptothrium rigidum* Kunth	Davidse 3281 (MO)	Jamaica, Kingston Parish	KF827794	KF827727	KF827662	KF827541
46	*Oropetium capense* Stapf	Venter 9939 & Venter (MO)	South Africa, Free State	KM011120	KM010917	KM010692	KM010324
47	*Pappophorum bicolor* E.Fourn.	Pohl 12464 (MO)	Mexico, Luis Potosí	KX582985	KX582914	KX582671	KX582397
48	*Pappophorum caespitosum* R.E.Fr.	Tivano 801 et al. (SF)	Argentina	–	–	–	JN175281
49	**Pappophorum pappiferum* (Lam.) Kuntze	Peterson 21689, Soreng, La Torre & Rojas Fox (US)	Peru, Ancash	GU360700	GU360276	GU359996	GU359128
50	*Pappophorum philippianum* Parodi	Renvoize 4225, Cope & Beck (MO)	Bolivia, La Paz	KX582986	KX582915	KJ768980	KJ768885
51	*Pappophorum vaginatum* Buckley	Wagner 3930 & Brown (MO)	Mexico, Durango	KX582987	KX582916	KX582676	KX582399
52	*Schmidtia kalihariensis* Stent	Goldblatt 8739A& Manning (MO)	Namibia, Keetmanshoop	**PV982182**	**PV982213**	**PV959321**	**PV954972**
53	*Schmidtia kalihariensis* Stent	Smook 10502 (MO)	South Africa, Northern Cape	**PV982183**	**PV982214**	**PV959322**	**PV954973**
54	**Schmidtia pappophoroides* Steud. ex J.A.Schmidt	Peterson 24182, Soreng, Romaschenko & Abeid (US)	Tanzania, Dodoma	**PV982184**	**PV982215**	**PV959323**	**PV954974**
55	**Schmidtia pappophoroides* Steud. ex J.A.Schmidt	Smook 10558 (MO)	South Africa, Northern Cape.	KM011124	KM010921	KM010697	KM010328
56	**Schmidtia pappophoroides* Steud. ex J.A.Schmidt	Zietsman 4082, Peyper, Seutloali & Tadi (MO)	South Africa, Orange Free State	**PV982185**	**PV982216**	**PV959324**	**PV954975**
57	*Sporobolus pyramidatus* (Lam.) Hitchc.	Peterson 21163, Saarela, Rosen & Reid (US)	Mexico, Durango	GU360628	GU360359	GU359910	GU359228
58	*Sporobolus virginicus* (L.) Kunth	Peterson 15683 & Soreng (US)	Chile, Region I	GU360610	GU360362	GU359892	GU359215
59	**Tetrachne dregei* Nees	Jarman 120 (US)	South Africa, Free State	GU360622	GU360365	GU359904	GU359218
60	*Tripogon chinensis* Hack.	Boufford 29012, Bartholomew, Chen, Donoghue, Ree, Sun Hang & Wu Su-Gong (MO)	China, Sichuan	KX583020	KX582946	KX582731	KX582451
61	**Triraphis mollis* R.Br.	Peterson 14344, Soreng & Rosenberg (US)	Australia, Western Australia	GU360669	GU360336	GU359933	GU359187
62	*Triraphis ramosissima* Hack.	Seydel 4278 (US)	Namibia	GU360651	GU360338	GU359931	GU359188
63	**Uniola paniculata* L.	Peterson 11160, Annable & Valdes-Reyna (US)	USA, Texas	GU360648	GU360341	GU359926	GU359192
64	*Zoysia macrantha* Desv.	Soreng 5913 & Peterson (US)	Australia, New South Wales	GU360641	GU360346	GU360017	GU359142

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Revision of the genus *Lasiacis* (Griseb.) Hitchc. (Poaceae, Paniceae, Boivinellinae)

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Abstract. A taxonomic revision of *Lasiacis* (Griseb.) Hitchc. 47 years since the last contribution (Davidse 1978) is proposed here. Historical and recent collections across 35 herbaria have been examined. Typifications are confirmed or emended, and 8 lectotypes are here designated (see Appendix III). Vernacular nomenclature and economic and therapeutic uses are updated based on bibliographic data or on information from herbarium specimens. For each taxon examined, an iconograph supporting the main diagnostic characters is proposed. Taxa previously described as varieties, such as *L. divaricata* var. *austroamericana*, *L. rugelii* var. *pohlii*, and *L. ruscifolia* var. *velutina* are elevated to the rank of species, and *L. acuminata* Swallen has been resurrected as a valid species, recognizing a total of 22 taxa, 18 species and 4 varieties.

Keywords: Boivinellinae, *Lasiacis*, Neotropics, Nomenclature, Paniceae, Poaceae, Taxonomy.

...if each biologist wishes to maintain a rich and interesting world to study ..., we cannot afford the luxury of ignoring those most basic of all biological skills-taxonomy and the knowledge of which species lives where (Pimm and Lawton 1998).

INTRODUCTION

Members of the genus *Lasiacis* (Griseb.) Hitchc. are widespread in various habitats of the Neotropics. (Fig. 1). *Lasiacis* was originally described as a section of *Panicum* L. by Grisebach (1864) and later was elevated to the generic rank by Hitchcock (1910) because of its distinctive characters, such as globose spikelets placed obliquely on the pedicels, obovoid fruits, pubescent at the apex and black/purple colored at maturity, palea abaxially concave and adaxially gibbous, oil production in the epidermis of the glumes, sterile lemma at maturity, and bamboo-like growth habit.

The first complete revision of *Lasiacis* was made by Hitchcock (1910). Sixty-eight years after Hitchcock's contribution in 1910, Davidse (1978) published a taxonomic treatment providing detailed information about the morphology, anatomy, and cytology of *Lasiacis*, focusing on polymorphism and phenotypic plasticity. One of the most controversial aspects is the number of taxa circum-

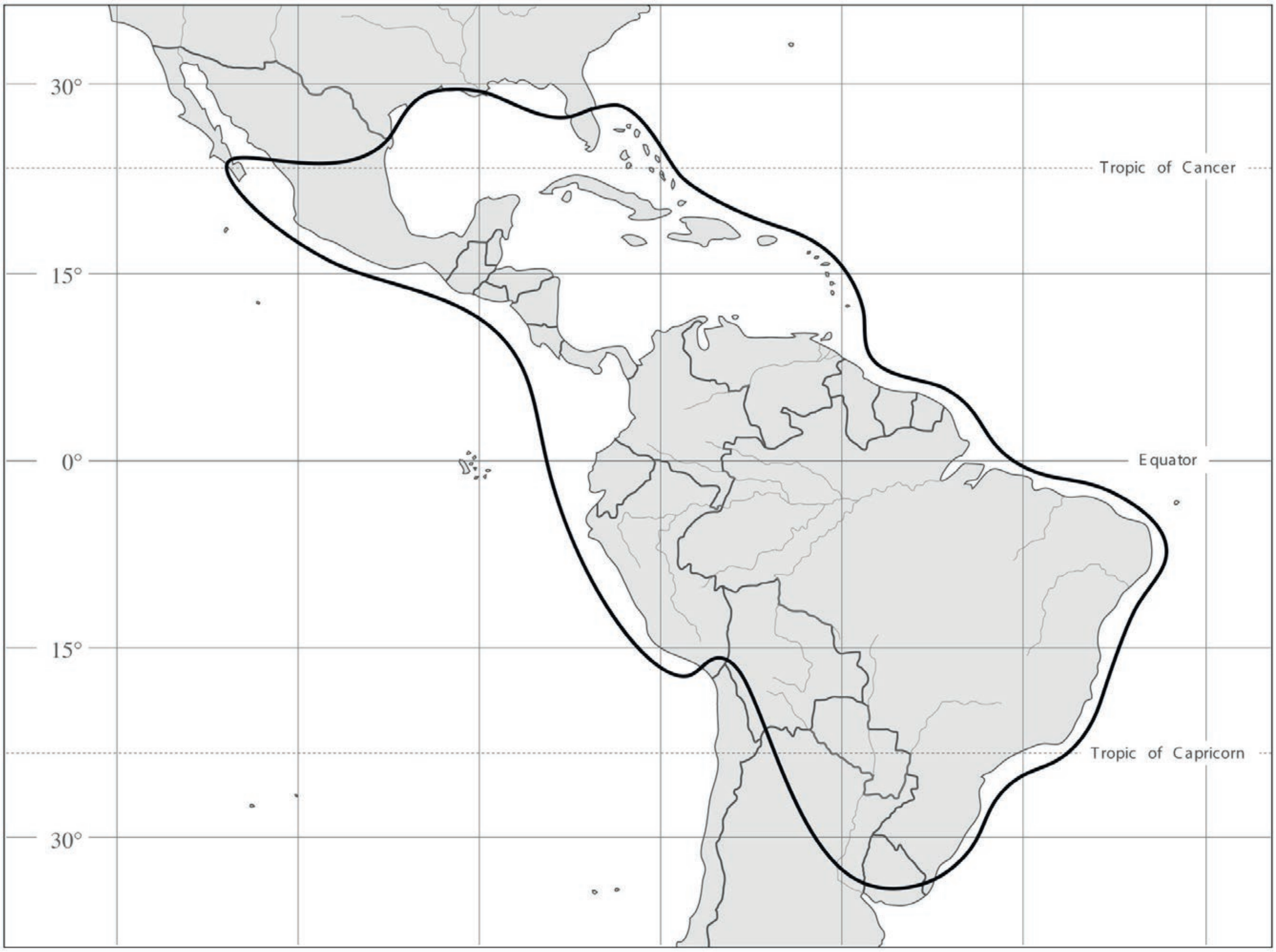

Figure 1. *Lasiacis* (Griseb.) Hitchc., general geographic distribution.

scribed in the genus. Hitchcock (1910) reported 15 species, while Davidse (1978) recognized 16 species and 13 varieties confirmed later by Webster (1988). In turn, Tzvelev (1989) recognized 25 species, and more recently 15 species were reported by Kellogg (2015) and Soreng et al. (2022). The uncertain number of the taxa in *Lasiacis* is due to the high morphological polymorphism and the potential degree of hybridization as observed by Davidse (1978).

This study is based on an exhaustive investigation of the herbarium and bibliographic documentation, and presents an updated taxonomic treatment as a starting point for further systematic studies.

Monographs and floristic treatments (Heywood 2001; Ebach et al. 2011; Lagomarsino and Frost 2020; Gorneau et al. 2022; Löbl at al. 2023) represent an improvement and a solid contribution upon which all biological works are based at any further level, reminding us the basic role of "*taxonomists and taxonomy*," which is often at risk of "*extinction*" and/or "*disappearance*" (Isely 1972; Baldini et al. 2021).

MATERIAL AND METHODS

This work is based on examinations of herbarium specimens viewed digitally, or *in-situ*, or via institutional loans by the author. The review of herbarium specimens is an important resource since it provides past and recent data, and often uncovers unique novelties (Heywood 2001; Bebber et al. 2010). Acronyms of the herbaria cited in the present work are according to Thiers (2016–): BM, BR*, C, CAS*, CEPEC, COL*, F*, FI (incl. FI-Webb herbarium), FT, FTG, G, HPZ, HUEFS, IJ#, K, L#, LAGU, LINN, MA, MHES, MO, NY, P, PI, PMA, RO, SCZ (= STRI), SD*, TO, UPS, US, USJ#, VEN#, VPI, W. (*) consulted online, (#) through loans. Specimens collected by the author and cited here has been deposited at CAY, FT, MHES, PMA, and SCZ, herbaria.

Typification is based on the original material according to McNeill (2014) and the current ICN (Turland et al. 2025). Although many digital images are available online, direct examination of the type material has proven to be preferable and more than an indirect evaluation. Type material is followed by the acronym of the herbarium (Thiers 2016–), the correspondent barcode and, in its absence, by the accession number. Descriptions are based on direct observations of the author compared with those reported by Hitchcock (1920) and Davidse (1978, 1994). Chromosome numbers when available are reported at the end of each description, and also in bold in the selected 'Specimens Section' including those from unpublished data reported in the herbarium labels. Vernacular names and ethnobotanical information are based on herbarium and bibliographical sources. General geographic distribution from bibliographic and online sources (GBIF, POWO, TROPICOS) are reported in a distinct section, and ecological observations are based on field observations as well as on herbarium specimens. Descriptive terminology follows Davidse (1978) and Beentje (2010).

In the 'Selected Specimens' section the countries of distribution for each taxon are listed alphabetically, and the specimens are in chronological order with the first collector followed by *"& al."* in case of more than two collectors.

The original drawings published here were created by Anne Maury (FT) and Michelle-Marie Nelson (US).

SPECIES AND VARIETY CONCEPT

In this revision I follow the morphological species concept of Davis and Heywood (1963: 91), "... *assemblages of individuals with morphological features in common and separable from other such assemblages by correlated morphological discontinuities in a number of features. The species in this sense is intended to be a collection of samples so similar that not only the describer, but other users would have little hesitation in saying they are alike, recognizable and communicable*", and as interpreted and commented in Minelli (1993: 63), Stuessy (2009: 144), and Stuessy et al. (2014: 296). The rank of variety here adopted is defined by a secondary variation with a morphological and geo-ecological correlations (White 1971).

GENERAL MORPHOLOGY

Roots and culms

The root system in *Lasiacis* is quite uniform and does not represent a character of systematic importance. In general, the roots are robust and often form long rhizomes (Figs. 2, 3). All species develop adventitious roots either at the basal nodes or at the culm nodes as well

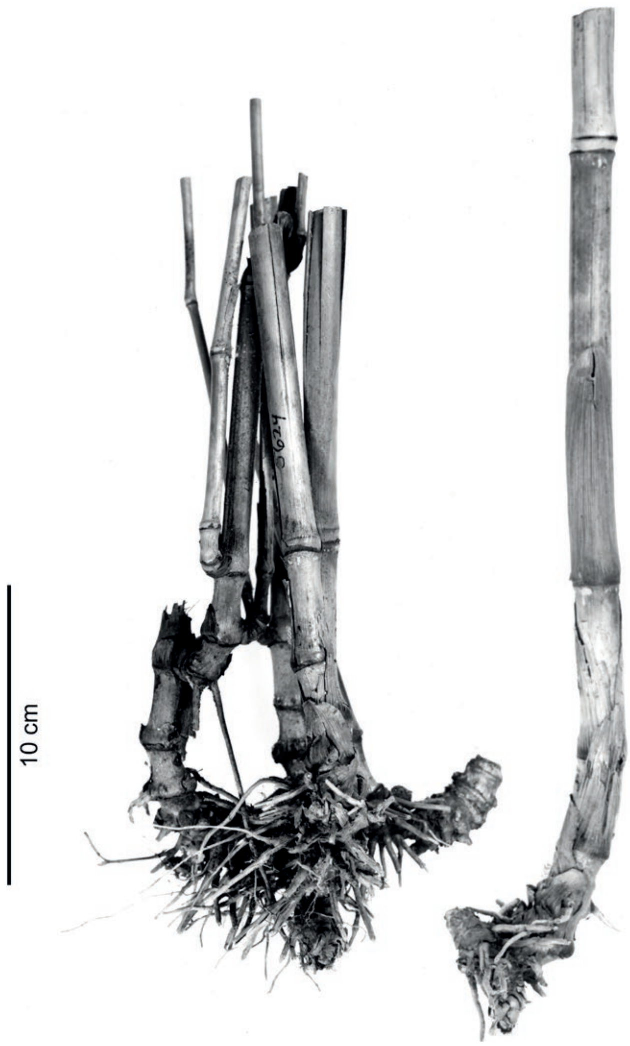

Figure 2. *L. maculata* (Aubl.) Urb., rhizomatous root system. [Colombia, *T.R. Soderstrom 1413* (US04285553)].

as robust prop roots [e.g., *L. maculata*, Panama, Coclé, Stapf et al. 828 (FT010893); *L. procerrima*, Panama, El Llano-Cartí, *Stapf et al.* 791 (FT010896)] at the base of the culm. A detailed description of the seedlings of *Lasiacis* according to the terminology of Hoshikawa (1969) is given in Davidse (1978). Several species have an erect habit while others are creeping and form long prop roots that remain unbranched above the ground (e.g., *L. grisebachii*, *L. sloanei*, *L. standleyi*).

Culms are often striking for their large size and woody habit, and can be 4–10 m tall (Fig. 4). The woody habit cannot be ascribed to a secondary growth, but only to a gradual accumulation of lignified primary tissue. Some species have a climbing or scandent habit, usually arching, and tend to lean on the nearby vegetation. Culm internodes can be either solid and pithy or par-

Figure 3. *L. maculata* (Griseb.) Hitchc., rhizomatous root system [Panama, Veraguas, *M. Stapf et al.* 844 (FT010891) photo R.M. Baldini].

Figure 4. *L. maculata* (Griseb.) Hitchc., general habit. In the foreground Dr. Richard S. Cowan. [Colombia, photo from *T.R. Soderstrom 1413* (US04285553)].

tially solid. Culm pulvini are present at the base of each internode and are strongly developed in all species.

Culms at maturity are clearly branched. A primary branch can produce several open secondary branches. Although Davidse (1978) does not attribute a diagnostic value to primary and secondary branching, in my opinion it can be useful for identification.

Leaves

Leaves in *Lasiacis* vary from linear-lanceolate (*L. linearis*, *L. oaxacensis* var. *oaxacensis*, *L. oaxacensis* var. *maxonii*) to elliptic, oval (*L. acuminata*, *L. anomala*, *L. divaricata* var. *divaricata*, *L. divaricata* var. *leptostachya*, *L. ligulata*, *L. maculata*, *L. rhizophora*, *L. ruscifolia*, *L. scabrior*, *L. sloanei*, *L. standleyi, L. velutina*). The sheath margins are free with a ciliate upper margin; the apex of the sheath can be extended as a narrow auricule. The elongated collar is called petiole or pseudopetiole.

A notable developmental variation feature is leaf pubescence which can be very common in secondary or tertiary branches and along the culm during the growth of the plant. The taxonomic value of leaf pubescence must be taken with care, depending on different causes correlated to the developmental, ecological or genetic factors. Some species have many different pubescence types, such as *L. maculata*, *L. nigra*, and *L. ruscifolia*.

Leaf shape in *Lasiacis* is strictly correlated to habitat of forest margin in the context of the "Forest Shade Clade" (see below Fig. 8). No-Kranz leaf anatomy is correlated with the C_3 photosynthesis pathway. A detailed description of the anatomy of the leaves in *Lasiacis* is given in Davidse (1978).

Inflorescences and spikelets

The inflorescence in *Lasiacis* is a panicle with a diagnostic taxonomic significance due to its size, mode of branching, and the arrangement of the spikelets (Hitchcock 1920; Davidse 1978). Except for *L. anomala*, all species of *Lasiacis* possess the *Panicum* type (Cialdella and Vega 1996; Zuloaga and Scataglini 2023), consisting of two glumes and two distichous florets alternately arranged on the rachilla. The lower or sterile floret bears a lemma, a palea, and sometimes a staminate flower with three stamens and two - sometime - rudimentary lodicules. The upper floret is fertile with a lemma, a palea, and two lodicules, three stamens and a branched stigma. At maturity the fertile floret becomes stiff with a tough surface.

An exception is represented by *L. anomala* whose spikelet differs in having an additional sterile lemma. The spikelet bears two glumes, two sterile florets (sometimes one of them staminate), and one fertile floret. This is a rare condition in the Paniceae found also in *Panicum quadriglume* (Döll) Hitchc. (Palacios 1968; Davidse 1978; Nicora and Rúgolo de Agrasar 1987; Cialdella and Vega 1996; Zuloaga and Scataglini 2023). (Figs. 5, 6, 7).

Distribution and ecology

Lasiacis is distributed in tropical and subtropical Americas, from the United States of America (Florida, Louisiana), the Caribbean area, through West Indies, Central America to Argentina (Hitchcock 1920; Davidse 1978; IPNI 2025; POWO 2025; TROPICOS 2025), covering the entire area of the Neotropical region (Cope

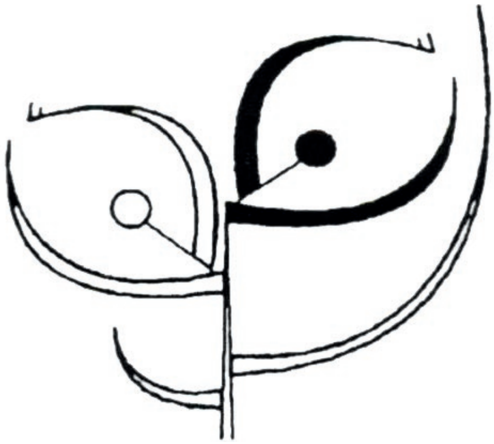

Figure 5. Spikelet structure in *Lasiacis* (Griseb.) Hitchc., staminate floret in white, perfect floret in black. [Modified from Cialdella and Vega (1996)].

Figure 6. Spikelet structure in *Lasiacis anomala* Hitchc., neutral floret dotted, staminate floret in white, perfect floret in black. [Modified from Cialdella and Vega (1996)].

2005) and most of its subregions (Morrone and Ebach 2022). (Fig. 1).

However, the global geographic distribution of *Lasiacis* has often been misunderstood. Clayton and Renvoize (1986), Watson et al. (1992) and Kellogg (2015) report its presence in Madagascar, erroneously including in the synonymy the genus *Pseudolasiacis* (A.Camus) A.Camus (Camus 1945) that is quite distinct from *Lasiacis* as pointed out in Bosser and Florens (1999), this excluding an intercontinental geographical disjunction of *Lasiacis*.

Lasiacis has a distribution range from sea level up to about 3500 m, preferring shady mesophytic forest margins and frequently growing deep into the forest. It often acts as

Figure 7. SEM photograph of the spikelet of *Lasiacis anomala* Hitchc. [Trinidad, *G. Davidse 2523* (L0797368), from Cannoni 2013].

a pioneer element in the ecological succession of secondary forests, including margins of the tropical savannah.

Due to its ecology, *Lasiacis* is often found with companion genera such as *Acroceras* Stapf, *Echinochloa* P.Beauv., *Oplismenus* P.Beauv., *Panicum* L. (subg. *Dichanthelium*, sect. *Cordovensia*), *Pseudechinolaena* Stapf to form the so-called "Forest Shade Clade" (FSC) as described by Giussani & al. (2001), Morrone et al. (2008) and confirmed by Teerawatananon et al. (2009) (Fig. 8). All taxa have large leaf blade, an indicator of habitats between forest and open areas (Gallaher et al. 2019).

Lasiacis is a C_3 grass, with a typically non-Kranz panicoid anatomy (Davidse 1978; Watson et al. 1992). Its presence even in C_4-dominated environments is related to its preference for shaded areas at the forest edge, and up to the montane heights to 3000–3500 m, where it increases its dispersal in more open areas (Giraldo-Cañas 2010). Recent phylogenetic studies have highlighted the uniform correlation between the genera belonging to subtribe Boivinellinae Pilg., and in particular to the "Forest

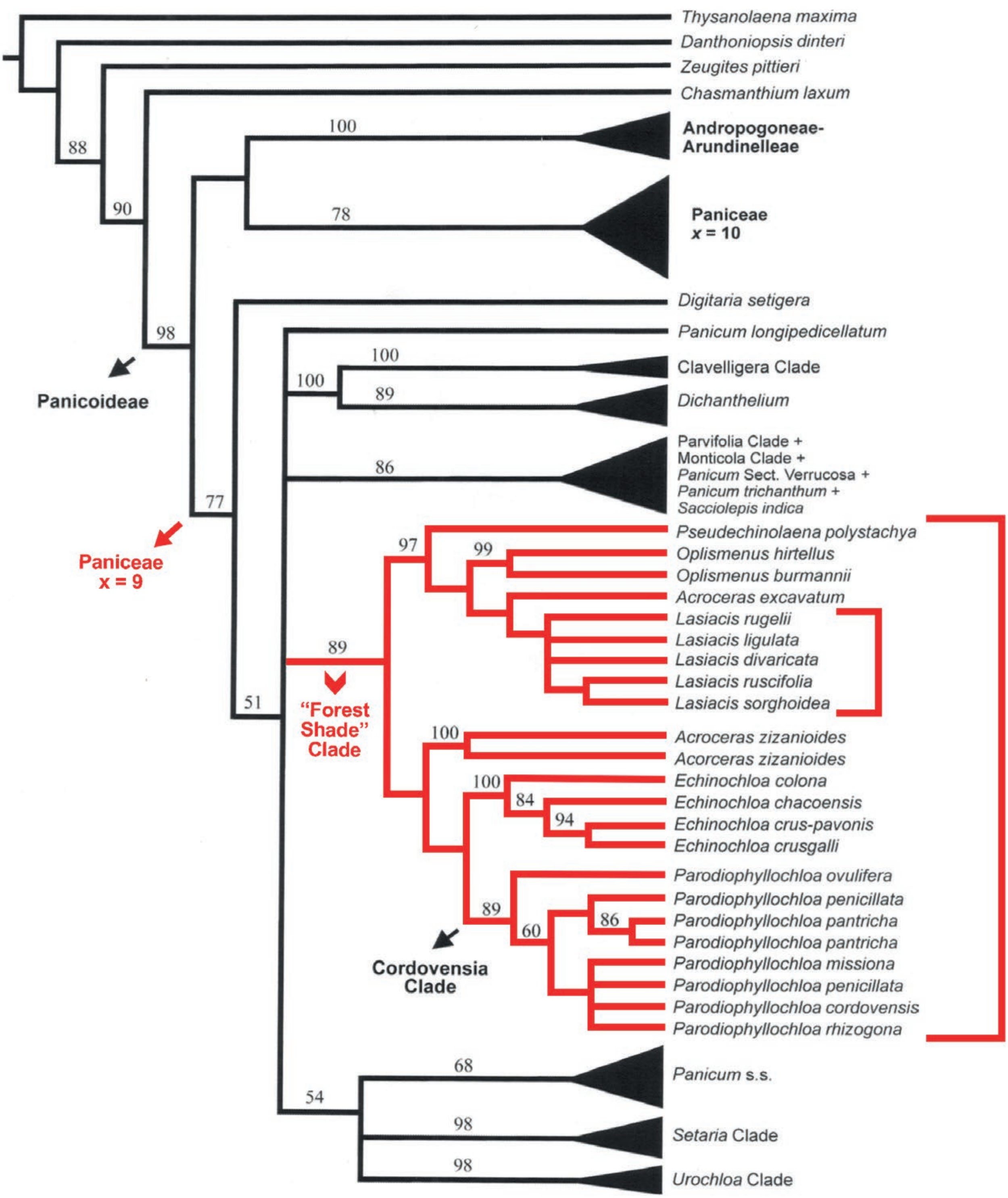

Figure 8. The "Forest Shade Clade" (Modified from Morrone et al. 2008).

Shade Clade", and C_3 photosynthesis, also including the genus *Alloteropsis* J.Presl as an example of reversion from C_4 to C_3 pathway (Ibrahim et al. 2009; Washburn et al. 2015; Hodkinson 2018). The Boivinellinae photosynthetic pathway can be summarized as follows: C_3, C_4 NADP-ME and C_3-C_4 intermediates (Morrone et al. 2011).

REPRODUCTIVE BIOLOGY AND CITOLOGY

As result of field and greenhouse observations Davidse (1978) recognized a mixed reproductive system within *Lasiacis* encompassing outbreeding and inbreeding pathways, the latter as dominant force, resulting in a minimal morphological variation within local populations. However, outcrossing among different populations is beneficial to guarantee a good level of genetic variability in a large spatial and geographical scale. Grasses are considered anemophilous, but tropical forest grasses, such as herbaceous bamboos as *Olyra* L., *Pariana* Aubl., *Piresia* Swallen (Gagné 1969; Soderstrom and Calderón 1971; Seres and Ramírez 1995; Gibson 2009; Saunders 2017), are visited by insects. During collecting trips in Panama, I saw some plants of *Cryptochloa variana* Swallen, *Pariana argentea* Davidse & Hollowell, and *L. maculata* visited by small diptera during anthesis when the stigmas were completely exerted. I assume this as an unspecialized and opportunistic pollination probably adequate to maintain high levels of genetic variability. Dórea et al. (2018) suggest a sort of insect-assisted anemophily in *L. ligulata*.

Paniceae have a base chromosome number of x = 9, 10 (Stebbins 1956; Davidse 1978; Gould and Shaw 1983; Hunziker and Stebbins 1987; Hilu 2004; Kellogg 2015). *Lasiacis* is typically a panicoid genus with $x = 9$ (Davidse 1978; Gould and Shaw 1983; Kellogg 2015). Davidse (1978) carried out accurate cytological investigations, reporting chromosome counts from natural populations of $n = 18$ and $2n = 36$, concluding a speciation event at the 4x level as a result of hybridization followed by polyploidization with subsequent stabilized diploidization (see Doyle et al. 2008).

DISPERSAL

In *Lasiacis*, as soon as the fruit is mature, the glumes and sterile lemmas become shiny black or purple and consequently attractive for bird dispersal (Davidse and Morton 1973; Snow 1981; Wheelwright et al. 1984; Davidse 1987; Cannoni 2013; Purificaçao et al. 2014; Fig. 9). The dispersal unit in *Lasiacis* is remarkably unique in Paniceae and can be considered basically as a black-purple, berry-like unit that attracts birds, which nourish from the oil present in the epidermis of the spikelet bracts. It can be argued that it is a result of a coevolutionary process due to an adaptative transition from a passive mode to an active mode via internal bird dispersal.

The relationship among the habitats of most *Lasiacis* species and the fruit eating birds (Davidse and Morton 1973) was revised and confirmed by Cannoni (2013) with a good correlation between the geographical distribution, habitat types of the *Lasiacis* species, and the behavior of the avian species during their nesting and frugivorous activities. Plant-frugivore interactions play a key role in the Neotropics and Caribbean islands and are useful in understanding the floristic distribution of native or introduced species (Vollstädt et al. 2022).

Figure 9. *Lasiacis nigra* Davidse: mature fruit black colored (Panama, Chiriquí, photo R.M. Baldini).

GENERAL PHYLOGENY AND BIOGEOGRAPHY

Lasiacis belongs to the PACMAD clade subfam. Panicoideae, tribe Paniceae, subtribe Boivinellinae Pilg. Butzin (1970a, 1970b) considered *Lasiacis* in the Paniceae belonging to the subtribe Microcalaminae Butzin exclusively on morphological characters, such as the presence of leaf blades with cross-veins, inflorescence type, compression of the spikelet, and lemma orientation (see also Davidse 1978), including genera such as *Oplismenus* P.Beauv. and *Pseudechinolaena* Stapf, typical of the “Forest Clade Shade”.

The phylogenetic position of *Lasiacis* within the subtribe Boivinellineae Pilg. is clearly supported by recent contributions (Morrone et al. 2011; Soreng et al. 2015, 2017, 2022; Kellogg 2015; Burke et al. 2016; Saarela et al. 2018). From the biogeographic and macro-evolutionary point of views, subtribe Boivinellinae, known as “Forest Clade Shade” in broad sense (Giussani et al. 2001; Hackel et al. 2018; Gallaher et al. 2022), is basal in the Paniceae, and includes grasses mainly living in shaded and forest edge habitats.

The origin of Boivinellinae is placed in the Tertiary between 27.65 and 21.92 Ma (Oligocene-Miocene) in

Madagascar and later spread to Asia and Central-South America including Caribbean areas (Hackel et al. 2018) and comprises C_3, C_4 as well as C_3-C_4 intermediate genera (Hodkinson 2018; Gallaher et al. 2022). The age estimation proposed by Hackel et al. (2018) agrees with that reported by Bouchenak-Khelladi et al. (2010).

Phytogeographic evaluation of the genus *Lasiacis* in the current neotropical scenario appears more complex. Davidse (1985) in his phytogeographic analysis of the Panamanian grasses, focused on the migratory movements between Central and South America. Bearing in mind the role of Panama as a land bridge in Oligo-Pliocene transition (Gentry 1982; Kirby and MacFadden 2005; Bacon et al. 2012; Graham 2010, 2011, 2018; Leigh et al. 2014) and paying attention to the fact that migration is not always unidirectional, it is, therefore, difficult to generalize migration patterns in a simplistic way. Davidse (1985) formulated the hypothesis of first differentiation of primitive creeping type species of *Lasiacis* in Central America from generalized woody type ancestral elements previously migrated from South America and followed by a counter migration of woody-like species to South America. Even if attractive, this hypothesis requires more solid phylogeographic support.

Undoubtedly, the current state of knowledge of *Lasiacis* includes species with a wide distribution in Central and South America (e.g., *L. maculata*, *L. ligulata*, *L. nigra*, *L. ruscifolia*), others mainly concentrated in Central America and the Caribbean region (e.g., *L. grisebachii*, *L. oaxacensis*, *L. pohlii*, *L. rugelii*), and with a localized distribution (e.g., *L. acuminata*, *L. harrisii* and *L. velutina*), and others showing a geographic vicariance divergence on continental scale (e.g., *L. divaricata* var. *divaricata* and *L. austroamericana*).

TAXONOMIC TREATMENT

Lasiacis (Griseb.) Hitchc., Contr. U.S. Natl. Herb. 15: 16. 1910. [see also Chase (1911)].

Panicum L. sect. *Lasiacis* Griseb., Fl. Brit. W. Ind. 551. 1864.

Type: *Panicum divaricatum* L., Syst. Nat., Ed. 10, 2: 871. 1759. – Lectotype, designated (as holotype) by Hitchcock and Chase, Contr. U. S. Natl. Herb. 22: 20 (1920).

Description

Perennial; shrubby grasses, often with woody culms, sometimes climbing onto trees, often rooting at the nodes. *Culms* erect, decumbent, open and branched; *internodes* solid or hollow, lignified. *Leaf sheaths* persistent with evident collars; *blades* pseudopetiolate to cuneate at the base, lanceolate to broader; *ligules* (0.4)4-5(-7.0) mm long, conspicuous or inconspicuous, glabrous, often reduced to a rim of hairs or densely pilose or pubescent. *Inflorescences* an open panicle, sometimes with deflexed branches, often densely spikeleted. *Spikelets* 3-6(-7.0) mm long, solitary, homomorphic, subglobose, ovoid, ellipsoid, oblique on their pedicels, deciduous; *glumes* and *sterile lemmas* generally broad, strictly apiculate, chartaceous, green and often black at maturity, nerved, glabrous, with a small tuft of hairs; *lower glumes* more or less 1/3 the length of the spikelet, several to many-veined; *upper glumes* and *sterile lemmas* subequal, about as long as spikelet, rounded on back; *lower paleas* small to well-developed, *lower floret* sterile or staminate; a second sterile lemma in *L. anomala*; *upper fertile florets* generally shorter than the spikelet, elliptical to obovate, shiny; *fertile lemmas* indurate, inclosing a membranous palea or a staminate flower, white, margins enrolled over the margins of the palea tending to be gibbous above, and concave below; both fertile lemmas and paleas wolly pubescent at their apices; stamens 3, styles 2, lodicules 2, fleshy and truncate. *Caryopses* ovate to obovate. *Chromosome number*: $n = 9$, $2n = 18, 36$. (Davidse 1972, 1978).

Etymology

From the Greek *lasios*, woolly, and *akis*, point, referring to the tuft of wool at the apex of the spikelet (Quattrocchi 2006; Clifford and Bostock 2007).

General distribution

From Southern United States of America (Florida, Louisiana), Central Mexico through the West Indies, Central America to South America up to northern Argentina (Davidse 1978; Kellogg 2015). (Fig. 1).

List of taxa

1 - *Lasiacis acuminata* Swallen, Mem. New York Bot. Gard. 9: 267. 1957.

2 - *Lasiacis anomala* Hitchc., J. Wash. Acad. Sci. 9: 1919.

3 - *Lasiacis austroamericana* (Davidse) Baldini

4a - *Lasiacis divaricata* (L.) Hitchc. var. *divaricata*, Contr. U.S. Natl. Herb. 15: 16. 1910.

4b - *Lasiacis divaricata* (L.) Hitchc. var. *leptostachya* (Hitchc.) Davidse, Ann. Missouri Bot. Gard. 64: 375. 1977.

5 - *Lasiacis grisebachii* (Nash) Hitchc., Bot. Gaz. (Crawfordsville) 54: 302. 1911.

6 - *Lasiacis harrisii* Nash, Torreya 13: 274. 1913.

7 - *Lasiacis ligulata* Hitchc. & Chase, Contr. U.S. Natl. Herb. 18: 337. 1917.

8 - *Lasiacis linearis* Swallen, Phytologia 4: 427. 1953.

9 - *Lasiacis maculata* (Aubl.) Urb., Symb. Antil. 8: 751. 1921.

10 - *Lasiacis nigra* Davidse, Phytologia 29: 152. 1974.

11a - *Lasiacis oaxacensis* (Steud.) Hitchc. var. *oaxacensis*, Proc. Biol. Soc. Wash. 24: 45. 1911.

11b - *Lasiacis oaxacensis* (Steud.) Hitchc. var. *maxonii* (Swallen) Davidse, Ann. Missouri Bot. Gard. 64: 375. 1977.

12 - *Lasiacis pohlii* (Davidse) Baldini

13 - *Lasiacis procerrima* (Hack.) Hitchc., Proc. Biol. Soc. Wash. 24: 145. 1911.

14 - *Lasiacis rhizophora* (E.Fourn.) Hitchc., Proc. Biol. Soc. Wash. 24: 145. 1911.

15 - *Lasiacis rugelii* (Griseb.) Hitchc., Bot. Gaz. (Crawfordsville) 51: 302. 1911.

16 - *Lasiacis ruscifolia* (Kunth in F.H.W. von Humboldt, A.J.Bonpland & C.S.Kunth) Hitchc., Proc. Biol. Soc. Wash. 24: 145. 1911.

17 - *Lasiacis scabrior* Hitchc., Proc. Biol. Soc. Wash. 40: 85. 1927.

18 - *Lasiacis sloanei* (Griseb.) Hitchc., Bot. Gaz. (Crawfordsville) 57: 302. 1911.

19 - *Lasiacis standleyi* Hitchc., Proc. Biol. Soc. Wash. 40: 86. 1927.

20 - *Lasiacis velutina* Swallen, Ceiba 4: 288. 1955.

Identification key of *Lasiacis* taxa
[adapted and amended from Davidse (1978)]

1. Spikelets with 2 glumes and 2 sterile lemmas . **2. *L. anomala***

1'. Spikelets with 2 glumes and 1 sterile lemma.

2. Culms solid, plants without a strong central cane, plants creeping or low-clambering, rooting at the nodes.

3. Ligules inconspicous, 03(–0.4)–1.1(–1.3) mm long, ciliate; leaf blades lanceolate, 7.0-18 cm long, 1.3(–1.5)–3.5(–4.0) cm wide .... **14**. ***L. rhizophora***

3' Ligules conspicuous, 1.5–6.0 mm long; leaf blades linear to lanceolate, 15–30 cm long, 0.7–2.5(–2.7) cm wide.

4. Leaf sheaths glabrous, spikelets paired or single clusters at the end of the panicle branches; lower floret staminate or not, lenght of palea subequal to the fertile floret.

5. Ligules 2.0–6.0 mm long... .... **11a. *L. oaxacensis*** var. ***oaxacensis***

5'. Ligules 0.5–1.0(–2.0) mm long... .... **11b. *L. oaxacensis*** var. ***maxonii***

4' Leaf sheaths puberulent; spikelets on long pedicels toward the end of the panicle branches; lower floret without a flower and palea 1/3–1/2 rarely 2/3 of the fertile floret........ ....**8. *L. linearis***

2' Culms entirely or partially hollow; plants creeping and rooting at the lower nodes, or erect, arching, climbing.

6. Plants creeping and rooting at lower nodes, ligules inconspicous with a ring of hairs, 0.3-0.5 mm long

7. Ligules inconspicuous, reduced to a ring of hairs, 0.3–0.5 mm long; palea of the sterile floret subequal to the lengh of the fertile floret ....**5. *L. grisebachii***

7' Ligules conspicuous, 4.5–7.0(–8.0) mm long, lacerate, slightly ciliate, palea of the fertile floret ½ the lenght of the fertile floret ....**19. *L. standleyi***

6'. Plants erect

8. Leaf blades cordate-clasping, 15–40(–45) cm long; lower nodes thick, hollow, with prop roots; inflorescences wide 20–120(–130) cm long...............................**13. *L. procerrima***

8'. Leaf blades not clearly cordate, smaller; without prop roots; inflorescence smaller, 2–30(–35) cm long.

9. Ligule evident, 3.5–7.0 mm long.

10. Panicle compact nearly spherical, up to 10 cm long, the base included in the upper sheath, rarely exerted; adaxial leaf surface scabrous; ligule up to 7.0 mm long ....**17. *L. scabrior***

10'. Panicle ovoid, 2–25(–30) cm long, usually totally exerted;

adaxial leaf surface glabrous to pubescent; ligule less tha 3.5 mm long.

11. Panicle branches ascending and widely spreading, and deflexed at maturity; leaf sheaths glabrous to pubescent; blades 5–18 cm long, (0.5–)1.0–3.0(–4.5) cm wide............... .... **7. *L. ligulata***

11'. Panicle branches ascending and less spreading, not delexed at maturity; leaf sheaths papillose-hispid, or pubescent; blades 5.0–24 cm long, 1.2–4.5 cm wide........**9**. ***L. maculata***

9'. Ligule not well visible, if evident less than 1.5 mm long.

12. Blades narrowly lanceolate, glabrous on both surfaces, sometimes with small hairs ....**3. *L. austroamericana***

13. Blades linear to narrowly lanceolate, 0.5-2.0 cm wide

14. Panicle with few spikelets; lower panicle branches reflexed or/and spreading; pedicels divergent at maturity; culms strongly arching, and clearly zigzag.. ....**4a. *L. divaricata*** var. ***divaricata***

14'. Panicle not as above, lower panicle branches not retroflexed; culms straight zigzag.

15. Spikelets 4.0–5.0 mm long

16. Base of panicle included in the sheath; pedicels and panicle branches short........... **4b. *L.divaricata*** var. ***leptostachya***

16'. Base of the panicle exerted; pedicels branches not as above, slender, spreading, flexuous.................... **10. *L. nigra***

15'. Spikelets 3.5–4.5 mm long.

17. Blades 0.8-1.0 cm wide, spikelets ovoid erected..................... ....**6. *L. harrisii***

17' Blades 0.5–3.0 cm wide......................**3. *L. austroamericana***

13'. Blades ovate-lanceolate, more than 2 cm wide.

18. Panicle open and sparsely branched, with few, large spikelets up to 5.0(–5.3) mm long.

19. Pedicels short, appressed; blades 1.5–5.0 cm wide,................ .... **18. *L. sloanei***

19'. Pedicels longer, spreading; blades 0.5–2.5 cm wide .... **10. *L. nigra***

18'. Panicle ovoid not clearly open, with many, smaller globose spikelets up to 4.0 mm long......................... **16**. ***L. ruscifolia***

12'. Blades pubescent at least on one surface.

20. Blades small, short and broad, ovate, 2–7 cm long, 0.5–3.0 cm wide.

21. Upper blade hispid, velutinous to pilose; panicle branches densely pilose.. **20. *L. velutina***

21'. Upper blade glabrous to puberulent, rarely pilose; panicle branches scabrid or puberulent, rarely pilose.

22. Culms papillose to pubescent, strongly zigzag; panicle branches deflexed; spikelets obovate, 4.5–5.0 mm long........ .... **15. *L. rugelii***

22'. Culms glabrous, not cospicuously zigzag, erect at the base; spikelets globose 3.5–4.4 mm long.....................**12. *L. pohlii***

20'. Blades larger, linear-lanceolate to acuminate, panicle open, large, often exceding the sheath.

23. Blades linear-lanceolate, ligule 0.5–2.0 mm long, spikelets obovate, 4.0–5.0 mm long, ... **10. *L. nigra***

23'. Blades acuminate, ligule 0.2–0.5 mm long, spikelets globose, 3.0–4.8 mm long.................................**1. *L. acuminata***

(1) *Lasiacis acuminata* Swallen, Mem. New York Bot. Gard. 9: 267. 1957. (Fig. 10).

Type: Venezuela, Territorio Amazonas, Great Rapids of the Orinoco, Isla Carestia at Saltos Carestia y Galio, 5 km north of Sanariapo, 100–120 m, erect to 2 m, 11 Nov. 1953, *Bassett Maguire, John J. Wurdack & George S. Bunting 36171* (holotype: US! [barcode US00134094]; isotype NY! [barcode NY00381281]).

Description

Perennials. *Culms* 2–6 m long, caespitose, erect and arching or clambering into shrubs, with slender branches as much as 50–60 cm long, 1–5 mm wide, upper part turned upward and climbing, glabrous, sometimes slightly dotted. *Leaf sheaths* mostly 3–5 cm long, generally longer than the internodes, pilose or hirsute toward the distal part, or nearly glabrous; *collars* villous, with margins ciliate, hairs 3.5 mm long; *ligules* 0.4–0.8 mm long, firmly membranous roundly ciliate, hairs 2 mm long; *blades* 3–8 cm long, 0.4–2.0 cm wide, lanceolate-acuminate densely ciliate on abaxial, less on the adaxial surface. *Panicles* 9–18 cm long, branches solitary, narrowly to widely ascending, few-flowered, scabrous. *Spikelets* 3.0–4.8 mm long obovate to subglobose; *lower glumes* 1.5–2.5 mm long, 5–7-veined; *upper glumes* 2.5–3.5 mm long, 3–6(–7)-veined, *sterile florets* staminate; *lemmas* 7–9-veined, *paleas* 1/3 the length of the fertile floret, *anthers* 2.5 mm long; *fertile florets* 2.5–4.0(–4.8) mm long, 1.8–2.8 mm wide; *anthers* 2.0–4.0 mm long, white, *stigmas* white. *Chromosome number*: n = 18 (Davidse 1978 as *L. sorghoidea*).

Distribution

Venezuela.

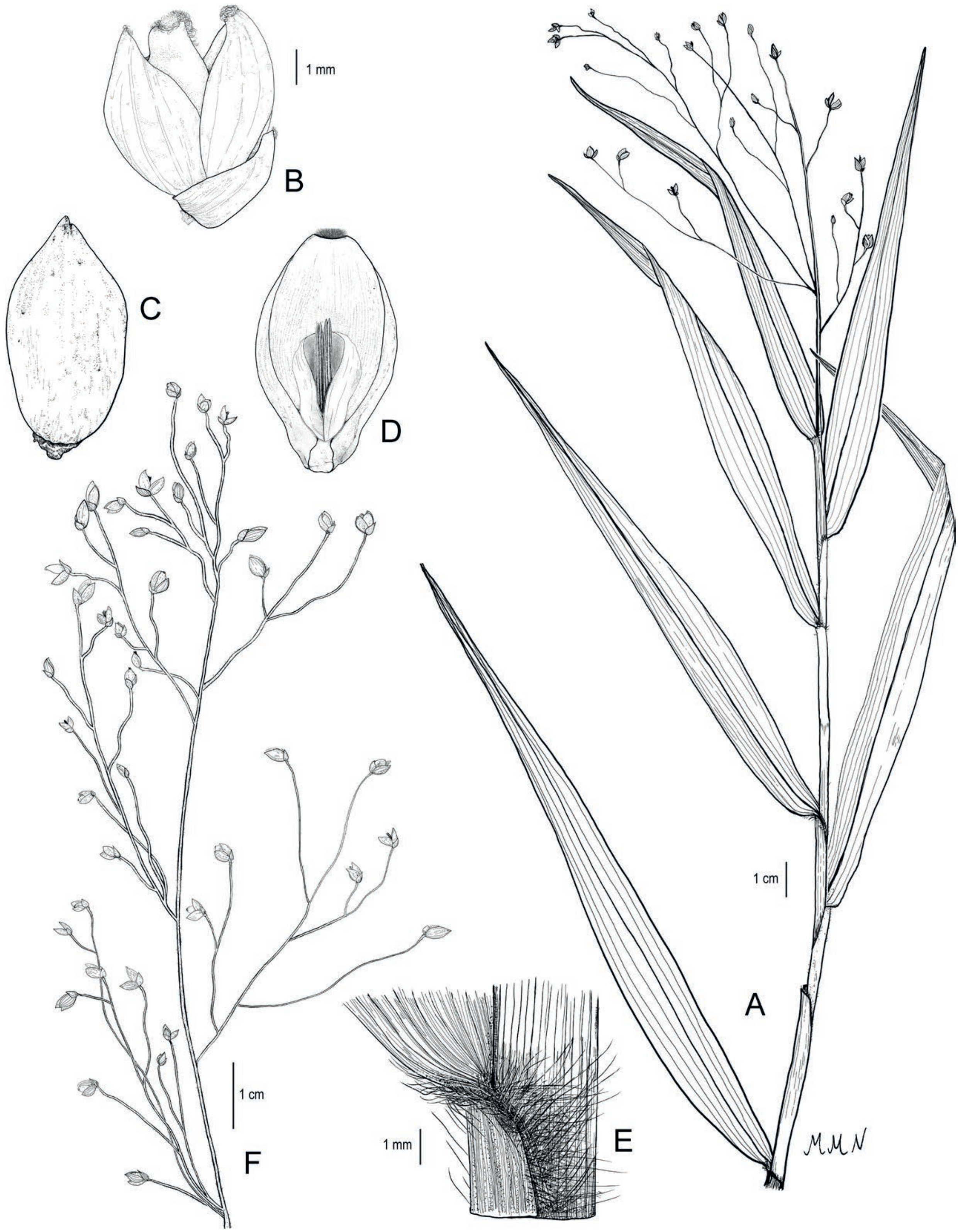

Figure 10. *Lasiacis acuminata* Swallen: **A**. Habit - **B**. Spikelet lateral view; **C**. Fertile upper floret dorsal view; **D**. Fertile upper floret ventral view with lower persistent palea; **E**. Ligular area; **F**. View of the upper culm [A-F. from the holotype: *Maguire et al. 36171* (US00134094)]. *Michelle-Marie Nelson delineavit.*

Distribution (bibliographic references)

Swallen (1957); Davidse (1978).

Ecology

Primary forest edges, roadsides, and very common also in secondary forest edges. 100-1500 m.

Phenology

October through May.

Remarks

Upon careful examination of the Venezuelan material, other characters confirm the validity of *L. acuminata* Swallen (Swallen 1957) such as: the ratio between inflorescence and terminal leaves, the open inflorescence with a smaller number of flowers if compared to *L. maculata*, the ratio between the persistent palea of the staminate flower and the maximum reduction of the ligule reduced to a ring of hairs.

Selected specimens

VENEZUELA. **Amazonas**. 12.5 km S of Puerto Ayacucho, 1 Nov. 1971, *G. Davidse 2785* (K, US); Isla Carestia, a small island in the Río Orinoco, ca. 5 km NNW of Sanariapo, 50 m, 3 Nov. 1971, *G. Davidse 2875* (MO), ***n* = 18!** (as *L. sorghoidea*, Davidse 1978); **Aragua**. Parque Nacional Henry Pittier NW of Maracay, Rancho Grande, 1150 m, 13 Nov. 1971, *G. Davidse 3047* (MO); 7.4 km S of Alto de Choroni (highest pt. on road) along road to Maracay, 1000 m, 14 Nov. 1971, *G. Davidse 3087* (MO); 5 km S of Alto de Choroni, along road to Maracay, cloud forest, 1200 m, 14 Nov. 1971, *G. Davidse 3103*, *3104* (MO); **Barinas**. 31 km NW of the Merita intersection (just outside of Barinas) along road to Merita, 550 m, 18 Nov. 1971, *G. Davidse 3184* (MO, US), ***n* = 18!** (as *L. sorghoidea*, Davidse 1978); **Bolívar**. Occasional on Isla Santa Elena, opposite of Río Pargueni, 80-90 m, 13 Dec. 1955, *J.J. Wurdack & J.V. Monachino 39855* (NY, US); La Gran Sabana, 49 km W of the intersection of the main road to Santa Elena and road to Cabanayen hillside with savanna on upper slope, forest in gully, 1360 m, 3 Dec. 1973, *G. Davidse & al. 4772A* (MO), *4782* (MO), ***n* = 18!** (as *L. sorghoidea*, Davidse 1978); **Caquetá**. 15 km SW of Belen along road to San José de Fragua (SW of Florencia), 400 m, 10 Jan. 1974, *G. Davidse & al. 5692* (MO), ***n* = 18!** (as *L. sorghoidea* var. *patentiflora*, Davidse 1978); **Distr. Federal**, 7.0 km SW of Carayaca by road, 1400 m, cloud forest area with much agricultural disturbance and 2nd growth, 6 Nov. 1971, *G. Davidse 2892* (MO), *2902* (MO), ***n* = 18!** (as *L. sorghoidea*, Davidse 1978); **Lara**. Distr. Jimenez, Parque Nacional Yacambù, Quebrada El Blanco, 1300-1400 m, 69°34'W, 9°43'N, 24 Oct. 1982, *G. Davidse & A.C. González 21062* (MO, NY); **Mérida**. 73 km NE of Mérida along the Mérida-Azulita road, 1400 m, 20 Nov. 1971, *G. Davidse 3241* (MO); **Miranda**. Selva de galería de la Quebrada Manzanares, afluente de la Quebrada Baryta, arriba de la Urb. Alto Prado, 10°26'N, 66°53'30''W, 1300 m, 8 Oct. 1980, *J.A. Steyermark & al. 123600* (MO); **Trujillo**. San Pablo de Mendoza, 1400 m, 19 Nov. 1922, *H. Pittier 10749* (NY, P, US).

(2) *Lasiacis anomala* Hitchc., J. Wash. Acad. Sci. 9: 1919. (Fig. 11).

Type: "*Trinidad, Fort Gorge Road, Port of Spain, edge of jungle, high climbing, with strong central cane, the branches not fascicled, main culm thick as a pencil, 27 November 1912, Hitchcock 9977* (= Am. Grass Natl. Herb. No. 595) (holotype: US! [barcode US00134096]; isotypes, BM! [barcode BM000938720], BR (photo!) [barcode BR0000006863166], C! [barcode C10017033], F (photo!) [Acc. No. 502308F], G! [barcode G00099527, G00176056 (two sheets)], GH (photo!) [barcode GH00023861], K! [barcode K000309325], L! [barcode L0797373], MO! [Acc. No. MO848755], NY! [barcode NY00381282], P! [barcode P00633948], PH (photo!) [barcode PH00016896], S (photo!) [Acc. No. 05-5476-S], US! [barcode US00134095], W! [Acc. No. W18890239913, W18890163754, W19220009719 (three sheets)].

(=) *Panicum divaricatum* L. var. *lanatum* Schlecht. & Cham., Linnaea 6: 33. 1831.

Type: "*Sieber 144*" (**lectotype, designated here**: HAL! [barcode HAL0106585]; isolectotypes: G! [barcode G00614199, G00614200], HAL! [barcode106584], L! [barcode L0797372], PI! [Acc. No. 041254]; US! [barcode US04319500]).

(=) *Panicum latifolium* L. var. *tomentellum* Döll in C.F.P.Mart. & auct. suc. (eds.), Fl. Bras. 2(2): 207. 1877.

Type: "*Brazil, Ceará, Gardner 1894*" (lectotype, designated by Davidse (1978: 1162): K! [barcode K000003999]; isolectotypes FI! [barcode FI012329], G! [barcode G00176055, G00176056, G00343686, G00343687 (four sheets)], NY! [barcode NY00863590], P! [barcode P00642273], US! [barcode US00956497, US00956498 (two sheets)], W! [Acc. No. W0005994, Acc. No. W0299446 (two sheets)]).

Description

Perennials. Culms up to 0.5-4 m long, 5-7 mm in diameter, woody, branching, erect at first and clambering over bushes and trees, glabrous. *Leaf sheaths* glabrous to more or less pilose at the margins, striate; *collars* silky-hairy; *ligules* 0.5-1.0 mm long, membranous, glabrous to short ciliate; *blades* 4-14 cm long, 1.5-3.5 cm wide, ovate-lanceolate to elliptic-lanceolate. *Panicles* 3-15 cm long, pyramidal, rachis and branches scabrous to puberulent, slightly reflexed. *Spikelets* 3-4 mm long, ovoid to globose; *lower glumes* 1-2 mm long, 0.5-0.7 mm wide, 7-veined; *upper glumes* 2-2.5(-2.8)

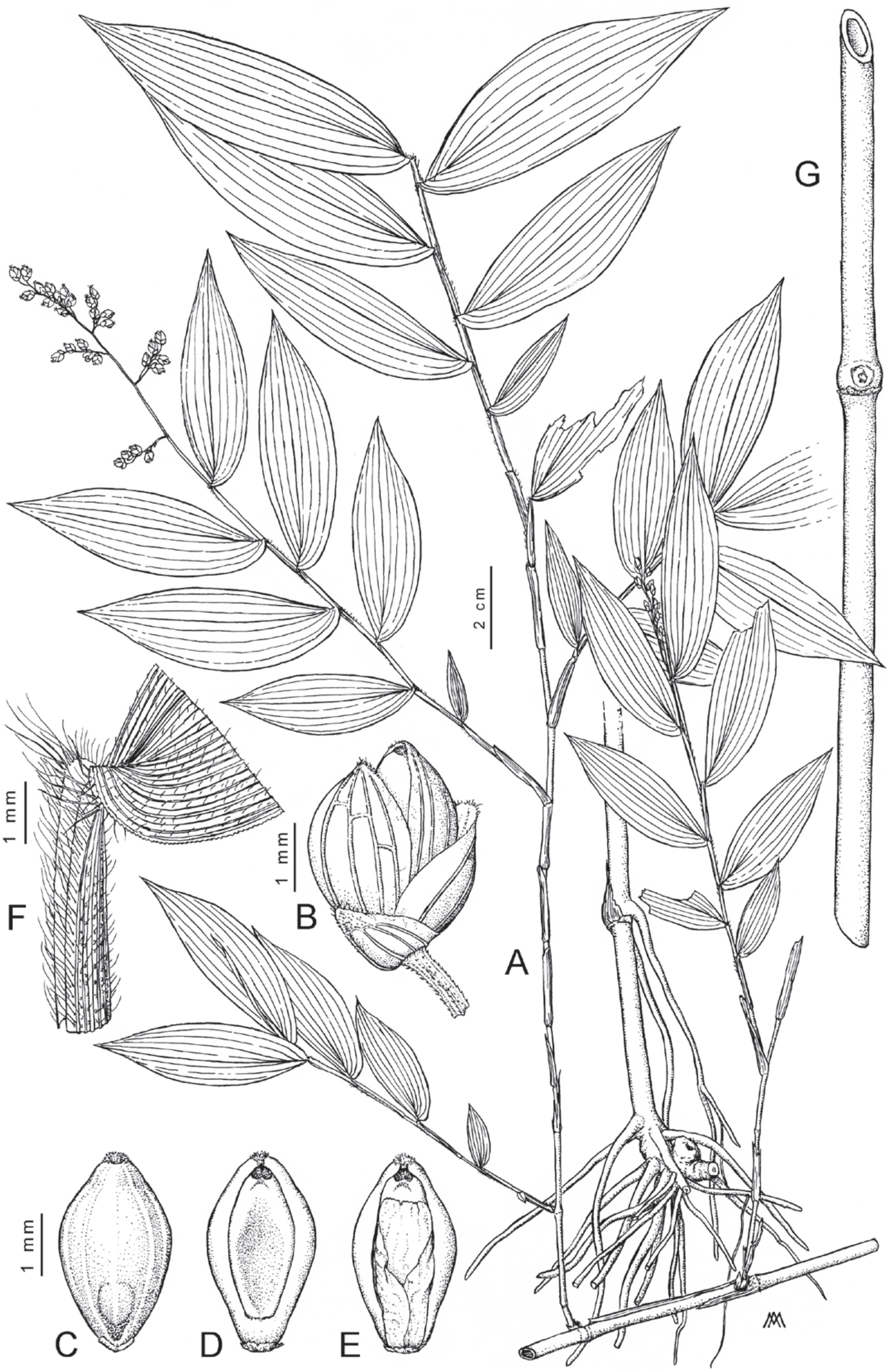

Figure 11. *Lasiacis anomala* Hitchc.: **A.** Habit [from *G. Davidse 2592* (L)] - **B**. Spikelet lateral view with two sterile lemmas; **C.** Fertile upper floret dorsal view; **D.** Fertile upper floret ventral view, without lower palea; **E.** Fertile upper floret ventral view with lower persistent palea; **F.** Ligular area [B-F from *G. Davidse 2523* (L)]; **G.** View of the culm [from *G. Davidse 2591* (K)]. *A. Maury delineavit.*

mm long, 0.7–1.0 mm wide, 9-veined; *first sterile lemmas* as long as the fertile floret, 9-veined, without a sterile palea; *second sterile lemmas* ½ to ¾ the length of the fertile floret, 9-veined, with a well-developed sterile palea sometimes with a staminate flower; *fertile upper florets* 2.5–3 mm long, 1.5–1.7 mm wide, *anthers* 1.5–1.8 mm long, white, *stigma* white; *caryopses* 2 mm long, 1.5 mm wide, ovoid-globose. *Chromosome number*: n = 18 (Davidse 1972, 1978).

Iconographs

Fig. 40A-B (Renvoize 1984); Fig. 53H (Judziewicz 1990); Fig. 87D (Renvoize 1998); Fig. 97 (Davidse 2004).

Vernacular names

Suriname: "*tamajoesji*" (Amshoff and Henrard 1948); "*bamboegras*", *J.C. Lindeman & al. 619* (K, NY, US), "*tamakushi*" (Judziewicz 1990); "*tamakusi*" van't Klooster et al. (2003); **Venezuela**: Lara, "*pistillo*" *R. Liesner & A. González 5532* (P) .

Distribution

Bolivia, Brazil, Guyana, Caribbean (St. Vincent, Barbados), Colombia, French Guiana, Guyana, Suriname, Trinidad & Tobago, Venezuela. (Fig. 12).

Distribution (bibliographic references)

Hitchcock (1919, 1920, 1936); Nash (1931); Amshoff and Henrard (1948); Hoyos (1985); Judziewicz 1990; Davidse (1978, 2004); Renvoize (1998); Zuloaga et al. (2003); Davidse et al. (2007); Hokchne et al. (2008); Giraldo-Cañas (2011); Villavicencio et al. (2014).

Ecology

Usually along shady forest edges, and savanna areas at the edges of forests. From sea level to 800-1200 m.

Figure 12. *Lasiacis anomala* Hitchc.: general geographic distribution.

Phenology

Plants with mature spikelets between April and December, sometimes also in February/March.

Remarks

The presence of an extra bract (sterile lemma) in the spikelet is undoubtedly the discriminating character that facilitates the identification. Both Hitchcock (1919) and Davidse (1978) consider this species very similar to *L. ruscifolia*. *Lasiacis anomala* has a range of distribution in northern South America. However, its diffusion into the Caribbean area cannot be excluded as supported by specimens from the Windwards Islands such as St. Vincent [*H.H. Smith 1976* (K. NY)], and Barbados [*F.W. Johnson 1246* (NY)].

Selected specimens

BOLIVIA. **Santa Cruz**. Florida, at La Angostura on Highway from Santa Cruz to Samaipata, 18°10'S, 63°31'W, 9 Jan. 1998, *M. Nee 47870* (NY).

BRAZIL. **Bahia**. Serra do Curral Feio, 16 km NW of Lagoinha, (which is 5,5 km SW of Delfino), 41°20'W, 10°22'S, 8 Mar. 1974, *R.M. Harley & al. 16991* (C, CEPEC, K, NY, P, US); Ribeira do Pombal, 19 May 1981, *G. Pinto 130/81* (CEPEC, HUEFS, US); Fazenda Boa Vista, Serra de S. José, Feira da Santana, 12°15'S, 38°58'W, 10 May 1984, *L.R. Noblick 3180* (CEPEC, HUEFS, K); **Ceará**. Aug.-Nov. 1838, *G. Gardner 1894* (G); Baturité to Guaramirango, 30 Apr. 1934, *J.R. Swallen 4419* (US); Campo Grande, 12-13 May 1934, *J.R. Swallen 4516* (P, US, W), *4587* (US); Serra de Baturité, sitio B, Inacio de Azevedo, 20 Apr. 1939, *J. Eugenio 284* (MO, US); RPPN Serra das Alams, Crateús, mata seca, 25 Mar. 2002, *F.S. Araújo 1378* (HUEFS); Crateús, Serra das Almas, 5°08'787''N, 40°55'651''W, 8 May 2002, *F.S. Araújo 1508* (HUEFS); **Goiás**. Río Araguaya, Campos Geraes de S. Vicente, 20 Jul. 1899, *L. Buscalioni 4079* (RO); **Maranhão**. Caxias to Barra do Corda, 18-26 Feb. 1934, *J.R. Swallen 3554* (US); "Ilha de Balsas", region between the Ríos Balsas and Parnaiba, about 30 km S of Loreto, 7°19'S, 45°07'W, 6 Apr. 1962, *G. Eiten & L.T. Eiten 4092* (MO); Loreto, a few hundred meters S of main house of Fazenda Morros, in gallery forest of the brook gully "Grota Grande", 22 Feb. 1970, *G. Eiten & L.T. Eiten 10750* (US); **Piauhy** (= Piauí). In sylvis stat frequens, s.d., *G. Gardner 3513* (BR); **Río Grande do Norte**. Municipio de Portalegre, Fazenda Cajazeiras, 06°02'S, 38°04'W, 3 May 1984, *A.C. Sarmento & J.S. de Assis 743* (K, NY); **Roraima**. Ilha de Maracá, Alto Alegre, SEMA Estação, 3°22'N, 61°20'W, 16 Jun. 1986, *M.J.G. Hopkins & al. 782* (K, MO, NY, US); Boa Vista, Estrada Confianças 1, 2°50'N, 60°40'W, 30 Jul. 1986, *J.A. Silva & al. 473* (MO, NY); Ilha de Maracá, Boa Vista, 18 May 1987, *J. Lima & B. Nelson 774* (K, NY); Ilha de Maracá, SEMA Ecological Reserve, 3°22'N, 61°26'W, 11 Jun. 1987, *W. Milliken 326* (K, NY).

COLOMBIA. **Meta**. Los Llanos, Río Meta, La Venturosa, 27 Oct. 1938, *J. Cuatrecasas 4191* (US); **Guainia**. Immediately S of Casuarito, lajas along the Río Orinoco, 90 m, 5°40'N, 67°37'W, 22 Jun. 1984, *G. Davidse & J.S. Miller 26374* (MO).

FRENCH GUIANA. Saül, 3°37'N, 53°13'W, 10 Feb. 1978, *J.M. Leeuwenberg 11763* (CAY); Roche Touatou, Bassin de l'Oyapock, 52°32'W, 2°57'N, 23 May 1995, *J.J. de Granville & G. Cremers 13048* (CAY, K, MO, NY); Moint Saint Marcel, zone SE du massif, 300 m, 2°23'N, 53°00' W, 27 Jul. 2002, *J.J. de Granville & al. 15518* (CAY, MO, P).

GUYANA. **Rupununi**. Path through forest between Yupukari and Karanambo, 12 Oct. 1963, *R. Goodland 955* (K, NY, US); Kanuku Mts., Rupununi R., slope of Breeze Mt. (Awartow), 3°05'N, 59°30'W, 11 Feb. 1985, *M.J. Jansen-Jacobs & al. 163* (CAY, K, NY, US); Rupununi River, Karanambo, 3°45'N, 59°20'W, May 1989, *P.J.M. Maas & al. 7150* (MO); NE slope of Mount Shiriri, 02°53'N, 059°43'W, 18 Jun. 1995, *M.J. Jansen-Jacobs & al. 4149* (K, NY, US); 1.5 miles S of Sand Creek, 3°00'N, 59°31'W, 21 Jun. 1989, *P.M. Peterson 7580* (CAY, NY, US); **Upper Takutu-Upper Essequibo**. Western extremity of Kanuku Mts., in drainage of Takutu River, 4-22 Mar 1938, *H.H. Smith 3131* (K, MO, NY, P, US); Kanuku Mts. ca. 10 miles NE of Sand Creek on N slope, 3°02'N, 59°25'W, 300-600 m, dense forest, 26 Jun. 1989, *P.M. Peterson 7637* (US); Rupununi area, Karanambo, 110 m, 03°53'N, 59°35'W, 17 Feb. 1990, *P. Acevedo-Rodriguez 3283* (US).

SURINAME. Tamakoesji (Kar), Tusschen rotsen by Wonotobo, Corantyn, 14 Oct. 1916, *G. Stahel 2854* (US); 8 km ca. in line from Paka Paka (Saramacca R.) to Ebbatop, 19 Feb. 1951, *J. Florschütz & P.A. Florschütz 1563* (NY); 9 km N of Lucie Rivier, 12 km W of Oost Rivier, 3°36'-3°41'N, 56°30'-56°43'W, 1 Aug. 1963, *H.S. Irwin & al. 54540,* 1 Sep. *55331,* 16 Jul. *54204* and 13 Sep. *55696* (K, MO, NY, P, US); Line Lucie R. - Wilhelmina Mts., 25 Jul. 1963, *Schulz 10464* (K); Zuid River, 2 km above confluence with Lucie River, 220 m, 3°20'N, 56°49'W, 3°10'N, 56°29'W, 16 Sep. 1963, *H.S. Irwin & al. 55790* (US); Area of Kabalebo Dam project., distr. Nickerie, 25 Nov. 1980, *J.C. Lindeman & al. 619* (K, NY, US).

TRINIDAD. 1877-80, *A. Fendler 963* (BM, K, NY, P); 4 Jun. 1908, *W.E. Broadway 2504 (*L, US); Trinidad, Mayaro, St. Margarets (Vallentines), 12 Jun. 1908, *W.E. Broadway 2627* (G, US); Trinidad, 1908, *A.S. Hitchcock 2564* (G, US); Chacachacare, 4 Dec. 1912, *A.S. Hitchcock 10063* (US); San Fernando, 9 Dec. 1912, *A.S. Hitchcock 10177* (US); Cedros, along banks in woods, 12-14 Dec. 1912, *A.S. Hitchcock 10136* (US, W); Port of Spain, 28 Dec. 1912, *A.S. Hitchcock 10001* (US); St. Joseph, 30 Dec. 1912, *A.S. Hitchcock 10021* (L, US); Lookout Hill, 7 Aug. 1919, *W.E. Broadway s.n.* (K, NY, US); St. Anns, 9 Sep 1920, *W.E. Broadway 5946* (K); Vicinity of Brighton, 12 Apr. 1921, *N.L. Britton 2905* (NY, US); Ietron Bay, 6 Oct. 1927, *W.E. Broadway 6775* (G, MO, US); Lopina Road via Arinea, 5 Aug. 1929, *W.E. Broadway 6736* (K, US); Pointe Gaude, 29 May 1932, *W.E. Broadway 8081, 8083* (K, MO, US); St. Augustine, 28 Jul. 1945, *Mogg 276* (K); St. George, along Morne Catherine Road, Chaguaramas Naval Base, 500-1000 ft, 27 Aug. 1959, *G.L. Webster & K.I. Miller 9943* (US); S of Point Fortin, Erin Savana, 24 Jun. 1963, *T.R. Soderstrom 1126* (K, NY, US); Area between the village of Piarco & the Piarco International Airport, 4 Aug. 1970, *G. Davidse 2522* (MO), *2523* (L, MO, NY, US), ***n* = 18!** (Davidse 1978); Rois Bay at the end of Chatman Road, 6 Aug. 1970, *G. Davidse 2580* (K, MO, NY, US), ***n* = 18!** (Davidse 1978); Along the Mausiga Road NE of parco, 7 Aug. 1970, *G. Davidse 2591* (K, MO, NY, US), *2592* (MO, L), ***n* = 18!** (Davidse 1978); Scotland Bay, sea level, 4 Aug. 1976, *C.D. Adams 14103* (NY); Claxon Bay, Solomon Hochoy Highway, 19 Sep. 1979, *C.D. Adams 601* (NY).

VENEZUELA. Venezuela, 13 Aug. 1891, *Eggers 13480* (US); **Amazonas**. 10-30 km al E de Puerto Ayacucho, 120 m, 5°35'N, 67°22'W, 11 Jun. 1977, *J.A. Steyermark & al. 113905* (MO, NY); **Anzoátegui**. Freites, Morichal Morichalote, 6-7 km al W del Río Oritupano, 110-220 m, 9°02'N, 63°30'W, 12 Jun. 1998, *Á. Fernández & al. 12764* (MO); **Atures**. 23 km NE of Puerto Ayacucho and 10 km E of Highway, hills and base of hills, near Cachama, 90 m, 5°51'N, 67°24'W, 17-19 Apr. 1978, *G. Davidse & O. Huber 15229* (MO); Carretera Puerto Ayacucho hacia Samariapo, 5°33'N, 67°35'W, 28 Nov. 1993, *A. Gröger 561* (MO); **Bolívar**. 1-10 km NW of Upata, on road to St. Felix, between Upata and Altagracia, 700 m, 31 Jul.-1 Aug. 1944, *J.A. Steyermark 57686* (NY, US); E of Miamo, Altiplanicie Nuria, 300-500 m, 8 Jan. 1961, *J.A. Steyermark 88215* (K, NY, US); Along Highway 19 between Calcara and Ciudad Bolívar, 24 Nov. 1973, *G. Davidse 4469* (K, MO, US); 13 km ESE of Upata along Highway 10 to Giasipati, 380 m, 2 Dec. 1973, *G. Davidse & al. 4617* (MO), ***n* = 18!** (Davidse 1978); San Pedro de las Dos Bocas, 24 Jul. 1978, *R. Liesner & A. González 5532* (P); Carretera Palito Blanco-Quiroz, en sitio 2 km al E del desvio hacia El Consejo, 23 Nov. 1978, *G.S. Bunting 6645* (MO); Distr. Cedeño vicinity of Panare village of Corozal, 6 km from Maniapure toward Calcara, 6°55'N, 66°30'W, 24 Se 1985, *B. Boom & M. Grillo 6070* (NY); Reserva Forestal Imataca, carretera Casa Blanca-San Martin de Turumban, 13 Jul. 1983, *B. Stergios & al. 5876* (MO); Isla en el Lago de Guri (Sector Las Carolinas), 15 km al E de la Presa R. Leoni, 7°40'N, 62°51'W, Aug. 1990, *G. Aymard & M. Norconk 8824* (MO, NY); Roscio, entre Parapaoy y El Purgo, 450 m, 6°35'N, 62°40'W, 5 Dec. 1992, *W. Diaz & J. Velazco 1253* (MO); El Callao, bosques entre El Calao y sector Chocó, entrando por La Ramona, 7°21'9"N, 61°55'06,5"W, 180-190 m, 21 Jul. 2009, *Á. Fernández & R. Gonto 26980* (NY); **Carabobo**. 2.5 km S of Puerto Ayacucho, small hill with one surface bare rock between road and the Río Orinoco, 1 Nov. 1971, *G. Davidse 2786* (MO); **Falcón**. Dist. Silva, Cerro Chichiriviche, entre La Luisa y La Soledad, 20-200 m, 6 Sep. 1974, *J.A. Steyermark & B.J. Manara 110955* (MO); "Casa del Golfete", parte Oeste del Golfete de Cuare, carretera a Tucacas, 23 Nov. 1993, *M.A. Martín Ballestreros MB127* (MA); **Guárico**. Road Calabozo-El Sombrero, 29 Aug. 1947, *H.M. Curran s.n.* (NY); Calabozo, Sep. 1963, *L. Aristeguieta 5135* (MO, NY); Estación Biológica de Los Llanos Calabozo, 6 Aug. 1966, *L. Aristeguieta 6212* (NY); Estación Biológica de Los Llanos, 10 km SSE of Calabozo, 60 m, 9 Nov. 1971, *G. Davidse 2916* (MO), ***n* = 18!** (Davidse 1978); Estación Biológica de Los Llanos, ca. 10 km SSE of Calabozo, savanna, 100 m, 3 Nov. 1973, *G. Davidse 3690* (MO, US), ***n* = 18!** (Davidse 1978); 54 km N of San Fernando de Apure along main Highway to Calabozo, patchy forest alternate with strips of wet savanna, now drying out, *Copernicia* palms prominent, 80 m, 10 Nov. 1973, *G. Davidse 3968* (MO, US); 80 km S of Las Mercedes along Highway 12 to Cabruta, 170 m, 20 Nov. 1973, *G. Davidse 4272* (MO), ***n* = 18!** (Davidse 1978); Miranda, Calabozo, 100 m, 8°45'54"N, 67°25'54"W, 22 Jul. 1976, *A. Castillo 584* (MO); Sabanas de la Estación Biológica de Los Llanos, 10 km SE a Calabozo, 200 m, 8°52'N, 67°22'W, 7 Aug. 1989, *F.O. Zuloaga & al. 4355* (MO); Estación Biológica de Los Llanos de la Sociedad Venezuelana de Ciencias Naturales, 12 km ca. SE de Calabozo, Edo. Guárico, 8°56'N, 67°25'W, 31 Aug. 1990, *N. Ramirez 2769* (NY); **Lara**. Palavecino, 16 km fuera de Manzanita, Hacia E Altar, 200 m, 15 Jul. 1978, *C. Burandt Jr. & R.F. Smith 281* (US); **Monagas**. Santa Barbara, 26 Oct. 1948, *B. Maguire & al. 27275* (US); **Yaracuy**. San Felipe, Veroes, fila montanosa 5 kms S de Bella Vista, 200-450 m, 10°23'N, 68°24'W, 11 Jul. 1973, *G. Agostini & al. 1808* (MO); **Sucre.** Carretera Carupano-El Pilar, 7 km N de El Rincón, 63°13'W,10°36'N, 6 Jul. 1972, *K. Dumont & al. 7405* (NY); Bordando el Golfo de Santa Fé, W de Santa Fé, en el sitio Punta Cochaima, 19 Aug. 1973, *J.A. Steyermark & al. 107854* (MO, NY); Montaña de Mochina, al S de Mochima, 20 km SE de Cumaná, 10°20'N, 64°20'W, 16 Sep. 1973, *J.A. Steyermark & al. 108440* (NY); Peninsula de Araya, 20 km NW of Cariaco, 2 km W of corner where road from Cariaco to Chacopata meets ocean, 0-100 m, 10°38'N, 63°40'W, 17-18 May 1981, *R. Liesner & A. González 12026* (K, MO, NY); Along Highway 9 between Cumuná and Barcelona, near border of the State of Sucre, 48 km E of Puerto Santa Cruz, 210 m, 10°16'N, 64°25'W, 30 Jul. 1982, *T.B. Croat 54399* (MO); **Valle**. 30 Jul. 1901, *O.O. Miller & al. 184* (BM, K, MO, NY, P, US); **Zulia**. 7 km E of Cupida, new road 1 km S of main road, starting at Río Chupaquire S of El Guacuco, 150 m, 10°09'N, 65°38'W, 16 May 1981, *R. Liesner & A. González 11882* (MO, US).

WINDWARDS ISLANDS. St. Vincent. Jul. 1888(?), *H.H. Smith 1976* (K, NY); **Barbados**. 3 Sept 1932, *F.W. Johnson 1246* (NY).

(3) *Lasiacis austroamericana* (Davidse) Baldini, **stat. nov.** (Fig. 13).

Bas.: *Lasiacis divaricata* (L.) Hitchc. var. *austroamericana* Davidse, Ann. Missouri Bot. Gard. 64: 374. 1977.

Type: *Brazil, Minas Gerais, near Santa Barbara do Caparaco, streamside, suffrutescent, 3 m high, climbing and rooting at lower joints, "canaviera", 21 Nov. 1929, Ynes Mexia 4007* (holotype: NY! [barcode NY0038128]; isotypes: BM! [barcode BM000938730], F (photo!) [Acc. No. 0046801F]; G! [barcode G00176057], GH (photo!) [barcode GH00023900], K! [barcode K001057518], MO! [Acc. No. MO144056], NY! [barcode NY00863558], P! [barcode P00642275], S (photo!) [Acc. No. S-S14-5165], SI (photo!) [barcode SI007516]; U (photo!) [barcode U0060705], US! [barcode US00134097], WIS (photo!) [barcode WIS0004162]).

(-) *Lasiacis divaricata* sensu Auct. Fl. S. America, non (L.) Hitchc.

Description

Perennials, caespitose. *Culms* up to 5-6 m tall, erect, progressively arching, scandent. *Leaf sheaths* glabrous, sometimes distally with few delicate hairs; *collars* glabrous, rarely puberulent with scattered small hairs; *ligules* 0.5-1.3 mm long, membranous, glabrous and ciliolate at the margins; *blades* 5-10(-15) cm long, 0.5-3.0 cm wide, narrowly lanceolate glabrous, acute to acuminate, the base asymmetrical, often proximally with small hairs on both surfaces, sometimes ciliate. *Panicles* 2-12(-15) cm long, with branches ascending to spreading at maturity. *Spikelets* 3-4 mm long, globose, purple-green when immature; *lower glumes* 1.5-3 mm long, 7-11(-12)-veined; *upper glumes* 2-4 mm long, 9-14-veined; *sterile floret* without flower or staminate, *lemmas* 9-11-veined, *paleas* ¾ to equal the length of the fertile floret; *fertile florets* 3-3.8(-4) mm long, 1.8-2.3 mm wide, *anthers* 2 mm long, white, *stigmas* white; *caryopses* 2-2.5 mm long, 1.7-2 mm wide. *Chromosome number*: $2n$ = 36 (Nuñez 1952 as *L.*

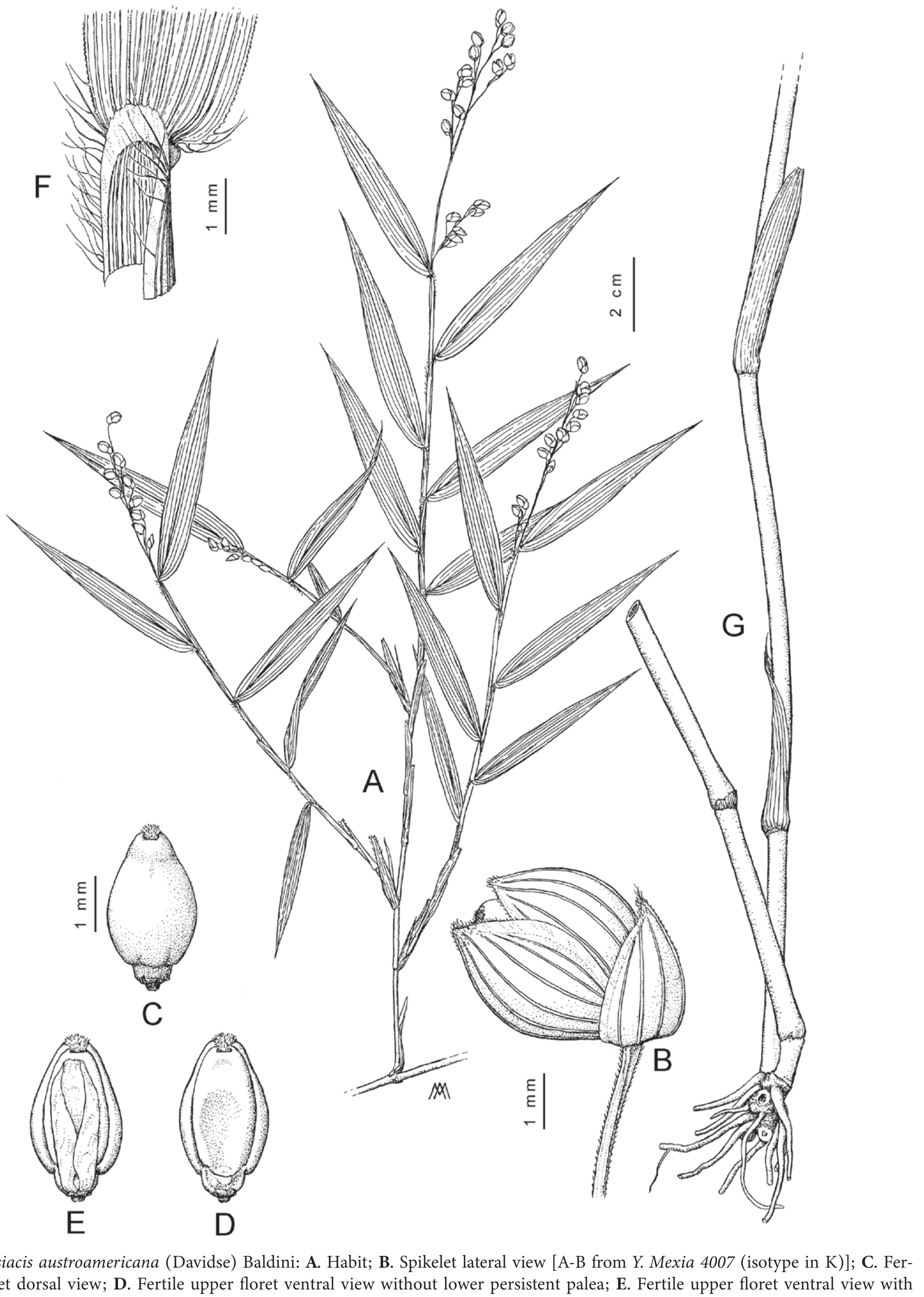

Figure 13. *Lasiacis austroamericana* (Davidse) Baldini: **A**. Habit; **B**. Spikelet lateral view [A-B from *Y. Mexia 4007* (isotype in K)]; **C**. Fertile upper floret dorsal view; **D**. Fertile upper floret ventral view without lower persistent palea; **E**. Fertile upper floret ventral view with lower persistent palea [C-E. from *E.D. Castellani & al. 150* (K)]; **F**. Ligular area; **G**. View of the culm [F-G. from *Y. Mexia 4007* (isotype in US001057518)]. *A. Maury delineavit.*

divaricata sensu Auct. Fl. Argentina); *n* = 18, *2n* = 36 (Davidse 1972, 1978).

Iconographs

Morrone and Zuloaga (2012: 333) as *L. divaricata* (L.) Hitchc. var. *austroamericana* Davidse.

Vernacular names

Argentina: "*caña*" (Quattrocchi 2006); **Brazil**: Minas Gerais, "*canaviera*" *Ynes Mexia 4007* (NY); **Paraguay**, "*takuapi'i*", "*takuarembo'i*", "*takuarembo'y*", "*tacuarilla*", "*tacuarita*", "*caña de cesto*" (Morrone and Zuloaga 1994a).

Distribution

Argentina, Bolivia, Brazil, Colombia, Ecuador, northern Argentina, Paraguay, Perú, Venezuela (see Fig. 15).

Distribution (bibliographic references)

Hitchcock (1920) as *L. divaricata* (L.) Hitchc. s.l.; Nash (1931) as *L. divaricata* (L.) Hitchc., s.l.; Davidse (1977, 1978); Morrone and Zuloaga (1994a); Cialdella and Vega (1996); Serrano and Terán (2000) as *L. divaricata* (L.) Hitchc. sensu Auct.; Garcia Santos and Takeo Sano (2001); Bussmann (2003) as *L. divaricata* (L.) Hitchc. sensu Auct.; Zuloaga et al. (2003); Renvoize et al. (2006); Hokche et al. (2008); Morrone et al. (2008); Giraldo-Cañas (2011) as *L. divaricata* (L.) Hitchc. sensu Auct.; Morrone and Zuloaga (2012); Villavicencio et al. (2014) as *L. divaricata* (L.) Hitchc. sensu Auct.; Pott and Pott (2021) as *L. divaricata* (L.) Hitchc. sensu Auct. When not indicated in the list above, the reference is as *L. divaricata* (L.) Hitchc. var. *austroamericana* Davidse.

Ecology

Secondary forests and brushy forest edges. Elevation ranges between 100 m to 1800 m above sea level.

Phenology

November through May/June.

Remarks

L. austroamericana is a geographical South American vicariant of *L. divaricata* which represents its related taxon with a Caribbean and Central American area of distribution. More comments are under *L. divaricata* var. *divaricata*.

Selected specimens

ARGENTINA. **Corrientes**. Chaco, Mayor Pedro La Gerenza, 11 Apr. 1978, *A. Schinini & E. Bordas 15187* (K); Dep. Santo Tomé, Ea. Timbó, en selva marginal del río Uruguay, 2 Mar. 1983, *A. Schinini & al. 23773* (HUEFS, US); **Guairá**. Ayo.Guazú, canino a San Gervasio, 56°17'W, 25°57'S, 27 Mar. 1993, *A. Schinini & al. 28045* (G); **Misiones**. Loreto, 30 Jan. 1908, *E.L. Ekman 618* (US); San Ignacio, 24 Feb. 1914, *H. Quiroga 24* (G); Misiones, Colonia G. Roca, 23 Jan. 1940, *A. Mutinelli 50* (US); Eldorado, 13 Dec. 1943, *A. Burkart 14728* (K, MO); Candelaria, Loreto, 2 Aug. 1944, *J.E. Montes 68* (W); Candelaria, 7 Jan. 1946, *J.E. Montes 1736* (K, US); San Ignacio, Puerto Viejo, 21 Mar. 1946, *G.J. Schwarz 2290* (FI); San Ignacio, 17 Apr. 1946, *G.J. Schwarz 2542* (W); Candelaria, Loreto, 12 May 1946, *J.E. Montes 2221* (K, US); San Ignacio, Puerto Mani, 20 Mar. 1950, *G.J. Schwarz 10232* (US); Candelaria, San Juan, 16 Dec. 1950, *J.E. Montes 15286* (K, MO); Depto. San Pedro, Montecarlo, 14 May 1951, *J.E. Montes 15401* (MO, US); Candelaria, 12 Apr. 1958, *J.E. Montes 27498* (C, MO, NY, US); Parque Iguazu, 25-30 Jun. 1963, *Del Puerto & Brescia 2663* (US); Bernardo de Irigoyen, 22 Feb. 1971, *A. Burkart 28253* (MO, US); San Pedro, 5 km a Tobuna, 26 Jan. 1973, *A. Schinini & A. Fernandez 6103* (G, P); San Pedro, Salto del Moconá, 10 Apr. 1979, *F.O. Zuloaga & al. 737* (US); Depto. Cainguas, Campo Grande, Ruta prov. 8, 13 Nov. 1995, *E.R. Guaglianone & al. 2817* (MO, NY); Libertador San Martin, Ruta Prov. 220, Parque Nacional Salto Encantado, 420 m, 27°03'S, 54°49'W, 11 Feb. 1996, *O. Morrone & al. 670* (MO, NY); General Manuel Belgrano, Parque Prov. Uruguaì, Ruta Prov. 19, 50 km de Wanda camino a Deseado, 260 m, 25°51'S, 54°10'W, 21 Apr. 1997, *O. Morrone & al. 1968* (MO, NY); Predio Guaranti, 26°54'S, 54°12'W, 27 Apr. 1999, *S. Tressens & al. 6108* (NY); San Pedro, Reserva Esmeralda, 480 m, 26°53'S, 53°54'W, 13 May 1999, *N.B. Deginani & al. 1302* (MO); Libertador General San Martin, 210 m, 27°05'S, 54°57'W, 26 Feb. 2000, *N.B. Deginani & al. 1479* (MO); **Salta**. Orán, camino de General Ballivan a Río Seco, 10 Dec. 1986, *F.O. Zuloaga & al. 2693* (K); San Martin, entre Coronel Corneo y Sierra de San Antonio, 12 Mar. 1987, *F. Zuloaga & O. Morrone 3045* (K, MO).

BOLIVIA. **Cochabamba**. Chapare, 8 Feb. 1929, *J. Steinbach 9091* (BM, G, K, MO, NY, US); **La Paz.** Yungas, 1890, *M. Bang 494* (G, L, US); Sur-Yungas, 21 Dec. 1923, *A.S. Hitchcock 22616* (US); Colaya, 1760 m, 14 Dec. 1935, *Y. Mexia 4307* (MO); La Paz, arriba de Puente Villa, Tarla Alto, 1850 m, 8 Mar. 1979, *G. Beck 395* (US); La Paz, 1.8 km SW of Yolosa on road to Chuspipata, 1400 m, 16°13'S, 67°45'W, 22 Mar. 1984, *J.C. Solomon & al. 12020* (MO, NY); Yungas, Alto Beni, 31 May 1995, *R. Seidel & al. 7793* (K); La Paz, Sud Yungas, de Chulumani 5 km hacia Irupana-Apa Apa, 16°21'S, 67°30'W, 13 Jan. 2000, *S. Beck 24751* (K); La Paz, Franz Tamayo, Senda Apolo-San José de Uchupiamonas, entre cima de Huacataya y arroyo Huacataya, 1955 m, 14°31'23"S, 68°18'23"W, 12 Mar. 2002, *T. Miranda & al. 443* (MO); La Paz, Bautista Saavedra, ANMI Apolobamba, Camata, puente sobre el Río Charazani-Camata, 1450 m, 15°13'39"S, 68°45'40"W, 19 Apr. 2005, *A. Fuentes & al. 6962* (MO); **Santa Cruz**. Andres Ibanez, 5 km S of Santa Cruz, 200 m, 22 Mar. 1981, *S.A. Renvoize & T.A. Cope 4024* (US); Andres Ibanez, 2 km W of La Belgica, 17°34'S, 63°14'30"W, 24 Jan. 1987, *M. Nee 33770* (MO, NY); Andres Ibanez, 7 km by air NW of Puerto Pailas, ca. 2.5 km W of center of Montero Hoyos, 300 m, 17°38'20"S, 62°50'30"W, 10 Feb. 1994, *M. Nee 44822* (MO); Florida between Samaipata and Las Cuevas, 4 Feb. 1996, *J.R. Wood 10551* (K); Santa Rosa de Lima, Quebrada del Creston, 1470 m, 17°52'S, 64°15'W, 3 Jul. 1996, *M. Saldias & A. Robles 4348* (MO, NY); Florida, along road to Bella Vista, 6.5 km SE from Santa Cruz-Samaipata Highway, 1275-1335 m, 18°13'S, 63°41'W, 27 Apr. 1998, *M. Nee & al. 49193* (MO, NY); **Santa Rosa**. Apr. 1892, *O. Kuntze s.n.* (NY); Lower Cocos, 31 Mar. 1902, *R.S. Williams 954* (NY); **Tarija**. Arce, 29.2 km S of Emboroza-Sidras, road on road to Bermejo, 12.7 km S of Naranjo Agrio, 600 m, 22°22'S, 64°29'W, 21-23 Apr. 1983, *J.C. Solomon 9879* (MO); Arce, Canton Emborozú, Reserva Natural Alarachi, 1020 m, 22°14'19"S, 64°34'25"W, 20 Sep. 2004, *M. Serrano & al. 4917* (MO).

BRAZIL. Bahia. 25 km NW de Feira de Santana, 12°10'00"S, 39°11'17"W, 13 Nov. 1986, *L.P. De Queiroz & M.J.S. Lemos 1008* (HUEFS, K); Abaíra, Mata do Engenho de Baixo, 13°19'S, 41°49'W, 2 Jan. 1993, *W. Ganev 1768* (CEPEC, HUEFS, NY); Municipio de Abaíra, Capão do criminoso, 950 m, 13°20'S, 41°47'W, 22 Jan. 1994, *W. Ganev 2846* (K, MO, NY); Brejões, Rod. Amargosa/Brejões ca. 28 Km, margem da rodovia, 13°3'47"S, 39°46'49"W, 25 Feb. 2000, *J.G. Jardim 2912* (CEPEC, HUEFS); Maracás, Fazenda Nova Esperança, 27 Feb. 2000, *R.P. Oliveira 365* (HUEFS); Encruzilhada, Rod. Encruzilhada/Ribeirão do Largo, 15°30'54"S, 40°48'51"W, 17 Aug. 2001, *A.M. Carvalho 6973* (HUEFS); Boa Nova, Fazenda Cotermaia, entrada à esq., ca. 1,2 km E de Boa Nova, na esorda para Dario Meira, mata seca, 14°22'25"S, 40°11'15"W, 8 Mar. 2003, *P. Fiaschi 1392* (CEPEC, NY); Maracás, deposi de Cruzeiro da cidade, Fazenda Juliana, 13°24'51"S, 40°24'37"W, 1016 m, 23 Apr. 2002, *R. Souza 159* (HUEFS); Maracás, fazenda de Roberto Pereira, 13°24'47"S, 40°24'28"W, 18 May 2002, *G.E.L. Macedo 41* (HUEFS); **Ceará**. Crato, 16 Apr. 1934, *J.R. Swallen 4356* (US); **Espírito Santo**. Iuna, 7 Feb. 1973, *G. Hatschbach & al. 31338* (K); Espírito Santo, Santa Maria de Jetibá, 13 Mar. 2003, *L. Kollmann 6048* (HUEFS). **Goiás**. São Domingo, 14 May 2000, *G. Hatschbach & al. 71073* (K); **Maranhão**. Barra da Corda to Grajahú, 1-5 Mar. 1934, *J.R. Swallen 3773* (US); Municipio de Loreto, Santa Barbara, 7°30'S, 45°3'W, 26 May 1962, *G. Eiten & L.T. Eiten 4736* (K, MO, NY); **Minas Gerais**. Caldas, 1844, *A.F. Regnell 308* (FI-Webb, P, UPS); Juiz de Fora, 24 Feb. 1925, *A. Chase 8619* (MO, NY, US); Viçosa, 11 Apr. 1925, *A. Chase 9437* (MO, NY, US); Serra do Caparõ, 30 Apr.-4 May 1925, *A. Chase 9644* (MO, US); Minas Gerais, 15 km N of Montalvania, 18 Mar. 1972, *W.R. Anderson & al. 37186* (C, K, MO, NY, P, US); Serra de São José, 12 Mar. 1994, *Válka Alves & Sarahyba 4430* (CEPEC, K); Santa Rita do Sapucaí, Serra da Bela Vista, 20 Feb. 1996, *O.S. Ribas 1326* (K); **Paraná**. Itararé, 16 Apr. 1910, *P. Dusén 9643* (G, MO, US); Paraná, Campo Morao, 28 Mar.-2 Apr. 1946, *J.R. Swallen 8959* (MO, US); Cab. Riberão do Tigre, Cerro Azul, 16 Dec. 1992, *G. Hatschbach & O.S. Ribas 58458* (C, G, HUEFS, K, W); Tunas do Paraná, 15 Dec. 1998, *Cruz & Abe 27* (W); **Rio de Janeiro**. Corcovado, Apr. 1839, *M. Guillemin 739* (G, K, UPS); Corcovado, Dec. 1840, *G. Gardner 5654* (K); Theresopolis, Serra dos Orgãos, 1 Mar. 1887, *J. Schenck 2947* (W); Rio de Janeiro, 1888, *A. Glaziou 17397* (C, NY, P, W); Rio de Janeiro, 1891, *A. Glaziou 18649* (C, K, US); Rio de Janeiro, 1894, *A. Glaziou 20574* (C, K, US); Petropolis, vale Bonsucesso, 13 Apr. 1968, *D. Sucre 2752* (MO, NY); Petropolis, Correias, Rio Bom Fim, Fazenda Bom Fim, base of Serra dos Orgãos, ca. 900 m, 22°27'S, 43°09'W, 3 Apr. 1972, *T.R. Soderstrom 1927* (MO, US); Paraíba do Sul, entre Queima Sangue e Salutaris, 24 Jul. 1984, *da Rocja & Peixoto 109* (K); **Rio Grande do Sul**. Arroyo Grande, 2 Mar. 1899, *C.A.M. Lindman s.n.* (G); Estación Linha Bonita, 19 Jan. 1949, *B. Rambo 40005* (MO, W); Lagoa da Pinguela p. Osorio, 27 Mar. 1950, *B. Rambo 46452* (MO, W); Buttenberg prope Montenegro, 22 May 1950, *B. Rambo 47132* (K, W); Tenente Portela-Derrubadas, 31 Jan. 1973, *J.M. Valls & al. 2580* (K); Boa Vista, Salvador do Sul, 24 Feb. 1976, *R.M. Klein 11735* (K); Sapiranga, 650 m, 18 Jun. 1989, *R. Wasum & al. 5961* (MA, MO, NY, US); **Santa Catarina**. Itapiranga, Chapecó, 3 Feb. 1951, *P.R. Reitz 3775* (NY), *17192* (L); Nova Friburgo, Feb. 1951, *Capell s.n.* (MA); Duque de Caxias, Ibirama, 200 m, 22 May 1956, *R. M. Klein 2026* (US); Itapiranga, 9 km W of Popí, on the road to Sant'Antonio, 200-350 m, 24 Feb. 1957, *L.B. Smith & al. 11783* (US); Alto Matador, 11 Sep. 1958, *P.R. Reitz & R.M. Klein 7079* (K, L, NY); Santa Catarina, Morro do Rio Vermelho, 300 m, 22 Jan. 1969, *R.M. Klein 8089* (US); **São Paulo**. 27 Dec. 1932, *F.C. Hoehne 29972* (K, P, US); São Manoel de Botocatì, 1870, *Gerdes s.n.* (W); São Paulo, 5 Mar. 1874, *H. Mosén s.n.* (P, US); Cerqueira Cesar, 400 m, Dec. 1898, *E. Gounelle s.n.* (G); São Paulo, mata do Jardim Botanico, 2 Jan. 1960, *O. Handro 910* (K, US); Cotia, 9 Apr. 1967, *T. Sendulsky 665* (HUEFS, NY); Ca. 38 km SW of Jacupiranga along Highway 116 to Curitiba, 680 m, 8 Mar. 1976, *G. Davidse & al. 10948* (MO), **n = 18!, 2n = 36!** (Davidse 1978); São Paulo, São Roque, 27 Sep. 1994, *L.C. Bernacci & al. 162* (HUEFS); São Paulo, Campinas, Fazenda Santa Elisa, 19 Jul. 1994, *S.L. Jung-Mendaçolli & al. 562* (HUEFS); Mandurí, 23°00'34"S, 49°21'25"W, 13 Jun. 1995, *J.Y. Tamashiro 1181* (HUEFS); Bauru, cerca de 5 km da cidade em direção a Agudos, 22°23'13"S, 49°01'25"W, 18 Mar. 1997, *E.D. Castellani & al. 150* (K).

COLOMBIA. **Boyacá**. Mt. Chapon, NW of Bogotá, 3400 ft, 14 Jun. 1932, *A.E. Lawrence 219* (BM, G, K, NY, US); Boyacá, Cordillera Oriental, afluente del Río Cusiana, abajo de Corinto, 24 Jun. 1967, *R. Jaramillo-Mejía 2753* (K); **Cundinamarca**. Juan Largo near San Antonio de Tena, 11 Dec. 1983, *J.R. Wood 4134* (K); Laguna Verde, La Capilla near Cachipay, 11 Nov. 1984, *J.R. Wood 4600* (K); Loma, La Cumbre, Vereda Chipatua, villetta-Guaduas, 18 May 1985, *J.R. Wood 4839* (K); Monte La Guarida, filo de la cordillera sobre La Carboneria, entre Las Brisas y Albán, 16 Oct. 1946, *J. Cuatrecasas 22174* (P); Villavicencio, Río Guatiquía, 20 Nov. 1948, *A. Molina* & *al. 18M.017* (K); El Valle, Km 51 carretera vieja Cali-Buenaventura, 400 m, 14 Feb. 1987, *X. Londoño & I.D. Quintero 177* (US); **Santander**. Between Suratà and California, 8-11 Jan. 1927, *E.P. Killip & A.C. Smith 16794* (NY, US); **Santa Marta**. 1898-1901, *H.H. Smith 2144* (G, K, L, P, W), *H.H. Smith 2148* (P); Cordillera de Santa Marta, San Andrés de la Sierra, 12 Jul. 1906, *H. Pittier 1650* (US).

ECUADOR. **Esmeraldas**. km 14-16 Lita-San Lorenzo, 78°33'W, 0°50'N, 750 m, 6 Jun. 1988, *S. Lægaard 71372* (G); **Morona-Santiago**. Pachicutza, 140 km on road Loja-Gualaquiza, tropical rain forest along Río Zamora, 78°34'W, 3°37'S, 26-27 Apr. 1973, *L. Holm-Nielsen & al. 4543* (NY); **Napo**. Along trail to Cascadas San Gabriel, 30 Jan. 1992, *S. Lægaard 101083* (K); **Napo-Pastaza**. Between Puyo and Canelos, Feb. 1935, *Y. Mexia 6850* (BM); Rocafuerte, Sep. 1969, *P.J. Edwards 207* (K); **Pastaza**. 5 km SE of El Puyo, 6 Oct. 1974, *J. Hudson 885* (K, NY); 18 km from Puyo on road to Tena, 3 Sep. 1976, *B. Øllgaard & H. Balslev 9260* (NY); Hacienda San Antonio de Baron von Humboldt, 2 km al NE de Mera, 1°27'S, 78°06'W, 27 Feb.-19 Mar. 1985, *D. Neill 5961* (NY, US); Pastaza, Road Puyo-Macas, 2 Dec. 1985, *S. Lægaard 53405* (K); Ca. 35-40 km along road towards Arajuno, 1°22'S, 77°43'W, 19 Sep. 1998, *S. Lægaard 19171* (MO); **Pichinca**. NE of Vincente Maldonado, Reserva de ENDESA, 79°02'W, 00°05'S, 7-8 Apr. 1984, *S. Lægaard 51921* (K, NY); NE of Vincente Maldonado, 79°02'W, 00°06'N, 29 Apr.-1 May 1985, *S. Lægaard 54202* (K, NY, UPS); NE of Alluriquin, 21 Jul. 1985, *S. Lægaard 54711* (K, NY); 13 km, of Alluriquin (32 km E of Santo Domingo) on new road to Quito, 5 Jun. 1990, *P.M. Peterson & E. Judziewicz 9533* (K); **Tungurahua**. Road Baños to Puyo, 22 km from tunnel at Agoyan, 78°13'W, 01°24'S, 1 Dec. 1984, *S. Lægaard 53395* (K, NY); **Sucumbios**. Along the road from Gonzales Pizarro to Río Dué, 27 Jan. 1992, *S. Lægaard 101029* (K);

Zamora-Chinchipe. Bombuscaro, 1000 m, 4°05'S, 78°57'W, 9 Mar. 1998, *S. Lægaard* & *al. 18533* (K, MO).

PARAGUAY. Plicomayo River 1888-1890, *T. Morong 1569* (K, MO, NY); **Alto Paraguay**. Cerro Cabrera, 5 Nov. 1992, *R. Fortunato & al. 3778* (G); **Alto Paraná.** S of Santa Lucia, 25°44'54"S, 54°59'48"W, 29 Feb. 1996, *E.M. Zardini & M. Vera 44839* (MO); **Caaguazú**. Feb. 1905, *E. Hassler 8920* (BM, G, K, NY, P, W); Caazapá, National Park Caaguazú, 450 m, 26°04'52"S, 55°30'24"W, 24 Nov. 1997, *E.M. Zardini & A. Benitez 47492* (MO); **Carapeguá**. Santa Barbara prés de Villa Rica, 27 Feb. 1876, *B. Balansa 40a* (K, L); **Concepción**. Arroyo Tagatiyá-Mi, 22°37'S, 57°32'W, 16 Mar. 1994, *E.M. Zardini & T. Tilleria 38918* (MO); **Guaira**. Tororo, Compania San Pedro, 25°55'S, 56°15'W, 15 Dec. 1988, *R. Gegen 1155* (MO); Road Melgarejo-Antena, 8 km S of Melgarejo, 25°55'S, 56°15'W, 5 Mar. 1989, *E. Zardini 11294* (MO); **Hayes**. Ruta Trans-Chaco, Río Monte Lindo, 14 Mar. 1979, *A. Schinini & E. Bordas 16582* (K); **Paraguari**. Parque Nacional Yvycui, 200 m, 14 Aug. 1980, *M. Vavrek 64* (US); Parque Nacional Ibicu'í, 26°00'S, 56°46'W, 4 Jun. 1989, *E.M. Zardini & R. Velasquez 12433* (MO).

PERÚ. **Cajamarca**. Huarango, San Martin-Quebrada Blanca, 860-900 m, 05°17'S, 78°43'W, 14 May 1996, *J. Campos & al. 2714* (MO); San Ignacio, La Coipa, localidad Vista Florida, Camino a La Laguna, 1900-2000 m, 05°26'10"S, 78°56'00"W, 20 Jun. 1997, *J. Campos & Z. Garcia 4062* (MO); Jaen, 11 km W of Highway 5N up Río Tabaconas and 4 km E of Tamborillo, 29 Mar. 2000, *P.M. Peterson & N. Refulio Rodriguez 15095* (K, MO). **Junín**. Pichis Trail, Enenas, 30 Jun.-2 Jul. 1929, *E.P. Killip & A.C. Smith 25615* (NY, US); **Loreto**, Maynas, carretera Iquitos-Nauta, km 21, trocha de penetracion al caserio Yarana, Río Nanay, ca. 120-150 m, 31 Jul. 1996, *M. Rimachi Y. 11761* (MO); **San Martin**. Mariscal Caceres, Distr. Tocache Nuevo, Río de La Plata, fundo del Sr. Manuel Gatica, 550-700 m, 12 Aug. 1980, *J. Schunke-Vigo 12146* (MO); **San Miguel**. Urubamba Valley, 1800 m, 26 May 1915, *O.F. Cook & G.B. Gilbert 923* (US).

VENEZUELA. **Aragua**. Near Aragua-Miranda border, Cordillera of Cerro Zamuro, S of La Fila Maestra of Interior Coastal Cordillera, NE of San Casimiro, 2-3 km NE of Hacienda Negrito, 29 km S of Cua, 875-1100 m, 26 Oct. 1963, *J.A. Steyermark 91783* (US); 8-9 km from the redoma at Cata Beach, SW towards Cuyaga, 400 m, 10°29'N, 68°42'W, 29 Sep. 1985, *B.K. Holst & al. 2300* (MO); **Lara**. Palavecino, 5-10 Aug. 1970, *J.A. Steyermark & al. 103639* (K, US, VEN); 16.3 km NW of Rancho Grande along road to Cata, 270 m, 15 Nov. 1971, *G. Davidse 3114* (MO); **Yaracuy.** Nirgua, SE de Nirgua, entre el Picacho de Ningua y el Caserio San Mateo, 1200-1400 m, 10°08"N, 68°38"W, 28 Dec. 2010, *W. Meier & N. Flauger 16903* (G, US); **Tovar**. Near La Victoria, 14 Nov. 1856, *A. Fendler 1613* (K); Near Caracas, 16 Aug. 1855, *A. Fendler 1614* (K); Between Caracas and La Guayra, 16 Aug. 1855, *A. Fendler 1615* (K); Valley of San Carlos River, 13 Apr.-10 May 1855, *A. Fendler 1617* (K); Between Maracai and Coroni, 12 Dec. 1856, *A. Fendler 2493* (K); Carayaca, Oct. 1908, *A. Jahn 312* (G, US).

(4a) *Lasiacis divaricata* (L.) Hitchc. var. ***divaricata***, Contr. U.S. Natl. Herb. 15: 16. 1910. (Fig. 14).

Bas.: *Panicum divaricatum* L., Syst. Nat., ed. 10, 2: 871. 1759.

Type: "*Habitat in Jamaica*", *Browne s.n.* (lectotype, designated by Hitchcock 1920, 20; See also Jarvis 2007: LINN 80.65!).

(=) *Panicum bambusoides* Ham. Prodr. Pl. Ind. Occ. 10. 1825.

Type: *Puerto Rico,* "*habitat in Am. Equinozi (P. Rico)*" (holotype: P! (Herb. Desvaux) [barcode P01176737]; isotype US! Fragment and photo from P [barcode US00148168]).

(=) *Panicum chauvinii* Steud., Syn. Pl. Glum. 1: 68 1854.

Type: Guadeloupe, *Duchassaing misit, 1851, s.n.* (holotype P! [barcode P00633950]; isotype US! Fragment from P [barcode US00148349]).

(=) *Panicum divaricatum* L. var. *stenostachyum* Griseb., Fl. Brit. W. Ind. 551. 1864.

Type: "*Panicum divaricatum* L. . *stenostachyum Gs., Jamaica*, *Mart. 20"* (holotype GOET! (photo!) [barcode GOET001982]; US! Fragment from GOET [barcode US00148441]).

(=) *Panicum divaricatum* L. var. *glabrum* Kuntze, Rev. Gen. Pl. 2: 784. 1891.

Type: "*West Indies, St. Thomas [Virgin Islands], Feb. 1874, O. Kuntze [55]* (**lectotype, designated here:** NY! [barcode NY00071095l] isolectotypes NY! (two sheets) [barcode NY00071096, NY00071097].

Description

Perennials caespitose. *Culms* erect (0.5-)1-6(-8) m long, strongly arching, often supported in brush, often procumbent when unsupported, the upper culm and primary and secondary branches clearly zig-zag; *branches* solitary or in group at the node; *internodes* 5-10 mm thick, glabrous, sometimes with a weak line of hairs on one side; *nodes* totally glabrous. *Leaf sheaths* glabrous, sometimes puberulent; *collars* usually puberulent, rarely pubescent to completely glabrous; *ligules* 0.2-0.5(-1) mm long, membranous, inconspicuous, usually not visible, ciliolate with a rim of hairs 0.2-0.6 mm long; *blades* 4-12(-15) cm long, 0.5-2.0 cm wide, linear-lanceolate, base shortly asymmetrical, adaxial surface glabrous, sometimes scabrid, abaxial surface glabrous, rarely puberulent. *Panicles* 2-15(-20) cm long, the longest branch up to 14 cm long, bearing spaced spikelets, lower branches reflexed. *Spikelets* 3-5(-6) mm long, obo-

Figure 14. *Lasiacis divaricata* (L.) Hitchc. var. *divaricata*: **A.** Habit [A. from *R. Garcia & al. 569* (NY)]; **B**. Spikelet lateral view; **C**. Fertile upper floret dorsal view; **D**. Fertile upper floret ventral view without lower persistent palea; **E**. Fertile upper floret ventral view with lower persistent palea [B-E. from *A.H. Liogier 17049* (NY)]; **F**. Ligular area; **G.** View of the culm toward the base [F-G. from *E.C. Leonard 3081* (NY)]. *A. Maury delineavit.*

vate; *lower glumes* (1.5–)2–3 mm long, 6-veined; *upper glumes* 2–4 mm long, 8-11-veined; *sterile floret* without a flower, *lemma* 8-13-veined, *paleas* subequal the length of the fertile floret; *fertile florets* 3.5–4.0 mm long, 2–2.5 mm wide, usually brown at maturity, *anthers* 2 mm long, whitish, *stigma* usually purple; *caryopses* 2–2.5 mm long, 1.6–2.0 mm wide. *Chromosome number*: $n = 18$, $2n = 36$ (Davidse 1972, 1978).

Iconographs

Tab. 29 as *Panicum divaricatum* L. (Kunth 1835); Plate 13 as *Panicum divaricatum* L. (Vasey 1884); Fig. 11 (Chase 1911); Fig. 1080 (Hitchcock and Chase 1950); Fig. 182 E-G (Acevedo-Rodríguez 2005); Davidse (2003: 391, 2007: 470); Lámina 155 (Catasús Guerra 2012b).

Vernacular names

Bahamas: "*wild cane*" *N.L. Britton & C.F. Millspaugh 2630* (NY), "*tibisee*", "*cane grass*", "*wild cane*" Acevedo-Rodríguez and Strong (2012); **Brazil**: Santa Catarina, "*taquari*" (Smith et al. 1982); **Cuba**: "*tibisi chico*" *M. Díaz-Piferrer s.n.* (FTG); "*pito de bejuco*" Hitchcock (1936), "*canutillo*", "*caña brava cimarrona*", "*cañita brava cimarrona*", "*caña bravilla*", "*cañabucillo cimarron*", "*pitilla de monte*", "*tibisí*", "*yerba brava*", "*pito de bejuco*", "*tibisí de sabana*" Acevedo-Rodríguez and Strong (2012), "*canutillo cimarron*", "*tibisí chico*", "*tibisí de monte*" (Roig 1963; Catasús Guerra 2012); **Haiti**: "*bamboo-marron*" (Urban 1912); **Mexico**: Baja California, "*carrizito*" (Rebman et al. 2016); Chiapas, "*yashal tzuzum (tzeltal)*" *Alush Mendez Ton 5027* (MO); Quintana Roo, "*xiat*" *M.E. Correa 6* (MO); "*carricillo*", "*carrizo*", "*carrizo de ratón*", "*ischcatichiya*", "*mehensit*", "*pichut*", "*pitut*", "*sit*" (Quattrocchi 2006); **West Indies**: "*small cane*", "*wild cane*" (Quattrocchi 2006).

Distribution

Bahamas, Belize, Costa Rica, Cuba, Dominican Republic, El Salvador, Guatemala, Haiti, Honduras, Jamaica, Puerto Rico, Leeward Islands, Mexico, Nicaragua, Panama, Virgin Islands, USA (Florida), Windwards Islands. (Fig. 15).

Distribution (bibliographic references)

Boldingh (1909) as *Panicum divaricatum* L.; Hitchcock (1909) as *Panicum divaricatum* L.; Hitchcock and Chase (1917); Hitchcock (1913, 1920, 1927a, 1936); Urban (1921); Nash (1931) pro parte; Standley and Calderón (1925); Schipp (1933); Standley (1937); Moldenke (1944); Swallen (1934, 1936, 1943, 1955b); Hitchcock and Chase (1950); Allan (1957); Adams (1972); Smith et al. (1982); Davidse (1978, 1994, 2001, 2003, 2007); Lindeman and Stoffers (1963); Beetle (1977); Fournet (1978); Howard (1979); Pohl (1980); Gould and Moran (1981); D'Arcy (1987); Cialdella and Vega (1996); Rogers and Holder (1999); Serna and López-Ferrari (2000); Morales (2003); Correa et al. (2004); Acevedo-Rodríguez (2005); Sutherland (2008); Acevedo-Rodríguez and Strong (2012); Catasús Guerra (2012a); Proctor (2012); Rebman et al. (2016); Villaseñor (2016); Sylvester (2017); Dávila et al. (2018); Sánchez-Ken (2019); Menjívar Cruz et al. (2021).

Ecology

A wide range of habitats such as hammocks (Florida) and pinelands; coastal xerophytic and mesophytic pine vegetation areas (cf. Mexico and Central America). From sea level to 800–1200 m above sea level.

Phenology

Flowering throughout the year, especially from June through April.

Remarks

Lasiacis divaricata var. *divaricata* is essentially a Caribbean species extending its range of distribution to Central America from Mexico until Panama. In South America it is represented by its geographical vicariant *L. austroamericana*, previously described as variety by Davidse (1977) and here elevated to the rank of species.

Selected specimens

BAHAMAS (**Lucayan Archipelago**). **Abaco**. Lubbers Quarters, 28 Dec. 1968, *W.T. Gillis 7338* (FTG); Great Abaco, Green Turtle Cay, in open coppice E of New Plymouth, 25 Nov. 1976, *D.S. Correll & H.B. Correll 47652* (FTG, MO); Great Abaco Island, ca. 5 mi. N of Dundas Town along main road, 14 Dec. 1979, *R.P. Wunderlin & al. 8302* (L, MO); Abaco National Park, 22 Jun. 2004, *E. Freid 04-109* (FTG); **Andros**. Coppice, near Deep Creek, long Bay Cays, Andros, 20–22 Jan. 1910, *J.K. Small & al. 8586* (K, NY, P, US); Along and near beach 1–2 miles S of Andros Town, 27 Feb. 1966, *E.Y. Dawson 26547* (US); Andros Island, N of Love Hill, 11 Jul. 1975, *S.R. Hill 3366* (FTG); North Andros Island, 20 May 1995, *Miller #B5* (C); North Andros, near path to Rainbow Blue Hole, 24°783516N, -77°.860733W, 5 Mar. 2012, *B. Jestrow 2012-018* (FTG); **Anguilla Islands**. Salt Key Bank, South End, 15–18 May 1909, *P. Wilson 8051* (K, NY); **Berry Islands**. Along Stede Bonnet Place, Great Harbour Cay, 16 Oct. 1974, *D.S. & H.B. Correll 43636* (FTG, NY); **Bimini**. May 1948, *R.A. Howard & E.S. Howard 10069* (FTG, NY); Near center of Cat Cay, 10 Jul. 1975, *D.S. & H.B. Correll 45609* (FTG); Congo Town, Ridge Coppice, 5 Mar. 1977, *R.P. Sauleda 1579* (FTG); **Cat Island**. 10 Jul. 1967, *R. Byrne 227* (FTG, NY); Just E of Zonicle Hill, 19 Nov. 1975, *D.S. Correll 46073* (FTG); **Crooked Island**. 9–23 Jan. 1906, *L.J.K. Brace 1617* (NY); **Eleuthera**. 18 Feb.–4 Mar. 1907, *E.G. Britton 6403* (NY); Eleuthera, The Current, vicin-

Figure 15. General geographic distribution of *Lasiacis divaricata* (L.) Hitchc. var. *divaricata* (dotted line) and *Lasiacis austroamericana* (Davidse) Baldini (solid line).

ity of the village and beach, primarily sand and coral, 27 Dec. 1969, *W.H. Lewis 7476* (FTG, MO); Eleuthera, about 1 mile S of John Millars, 15 May 1975, *D.S. Correll & S.R. Hill 45128* (FTG); North Eleutheria Airport, 15 Dec. 1979, *R.P. Wunderlin & al. 8445* (MO); Wemyss Bight Area, 24°072'N, 76°12.867'W, 2 Nov. 2006, *M.A. Vincent & C. Kwit #13300* (FTG); **Exumas**. Hummingbird Cay, 14 Jan. 1969, *N.H. Nickerson 2952* (FTG); Great Exuma, Flamingo Bay, area just E of George Town, 11 Dec. 1973, *D.S. Correll 40919* (FTG); **Great Bahama**. 5-13 Feb. 1905, *N.L. Britton & C.F. Millspaugh 2630* (NY); Long Cay, 7-17 Dec. 1905, *L.J.K. Brace 4230* (NY, US); Near Russel Town, 4 miles from Freeport, 31 Mar. 1969, *W.T. Gillis 7769* (FTG); **Inagua**. 21 Oct. 1904, *G.V. Nash & N. Taylor 1240* (NY); **Long Island**. 1 mile W of the Queen's Highway on the Galloway Road, South Clarence Town, 23 Jun. 1974, *S.R. Hill 2289* (FTG, MO, NY); Long Island, S of Clarence Town, 23°04'00"N, 74°55'00"W, 16 Aug. 1998, *L. Richey 98-246* (FTG); **Mayaguana**. SW of Airport, 4 Jan. 2006, *E. Freid 06-048* (FTG); **New Providence**. Coppice, Farringdon Road, 24 Aug. 1904, *N.L. Britton & L.J.K. Brace 187* (K, NY, US); New Providence Island, 25 Dec. 1963, *J. Merilainen & K. Roe 36* (US); 1 mile S of Foxhill, 1 Nov. 1973, *D.S. Correll & et al. 40321* (FTG, MO, NY); New Providence Island, along N side of West Bay Street, at Love Beach, 7 Sep. 1983, *P. Ruben & D.K. Sauleda 8418* (FTG, MO); New Providence Island, Clifton Heritage Park, 29 Dec. 2006, *E. Freid 06-761* (FTG); **Rose Island**. 27-28 Jan. 1905, *N.L. Britton & C.F. Millspaugh 2130* (NY, US); **San Salvador**. 25-26 Feb. 1907, *N.L. Britton & C.F. Millspaugh 5696* (NY); Watlings Island, northeast End, 27-28 Nov. 1907, *P. Wilson 7309* (K, NY); N of Pigeon Creek, 1 Jan. 1970, *W.T. Gillis 8789* (FTG); San Salvador Island, SW of Flamingo Pond, 4 Dec. 1973, *Fernandez & al. 84* (FTG); San Salvador Island, 22 Nov. 1974, *D.S. Correll 43906* (FTG); **Turks & Caicos**. North Caicos, Kew and vicinity, 1 Mar. 1911, *C.F. Millspaugh & C.M. Millspaugh 9132* (NY); Caicos, along road near St. James' Hill, 1 Sep. 1974, *D.S. Correll 43383* (FTG); Caicos Islands, Providenciales, Turtle Cove area, 16 Dec. 1975, *D.S. Correll 46438* (FTG); Turks and Caicos Islands, Middle Caicos, Bambarra, North end of MC6 trail, 16 Nov. 2000, *B.N. Manco 14* (FTG, K); North Caicos Island, Kew, edge of footpath through town of Kew, 7 Sep. 2002, *J.L. Sadle #115* (FTG); Turks and Caicos Islands, North Caicos, Bottle Creek, Quary Pit Road, 21°91'20"N -71°9'35"W, 29 Mar. 2006, *M.A. Hamilton 480* (K, FTG).

BELIZE. Belize. Belize, 172 mile South of Rockville Quarry on road to Sibun River, (coarse climbing grass on forest trees, occ. in extremely dense secondary forest on heavy clay soil over limestone), 28 Nov. 1968, *R.R. Innes RRI 58* (K); Belize, Gracie Rock, 1.5 miles S of Mile 22 Western Highway, 5 Jun. 1973, *J.D. Dwyer 10971* (MO); Belize, vicinity of Maskall River, 6 Jun. 1973, *T.B. Croat 23924* (MO, NY, US); Belmopan, 5 Mar. 1974, *W.C. Verboom 5075* (MO, P); **Cayo**. Commune Ridge, 1936, *C.L. Lundell 6430* (NY, US); Vaca, 11 Mar. 1938, *C.L. Lundell 2332* (K, NY, US); Cayo, Sep. 1964, *Disney A380/D* (BM); Cayo, ca. 250 m W of Hummingbird Highway, at a point ca. 2,5 miles of S of junction with Western Highway, 50 m, 17 Jul. 1970, *D.L. Spellman & W.W. Newey 1713* (MO); Cayo, 2 miles S junction W Highway & Hummingbird Highway, 27 Jul. 1971, *R. Wunderlin & al. 322* (MO); Vicinity of Milionario between the McCal River and Cuevas, disturbed forest and roadside, 1900 feet elev., 30 May-3 Jun. 1973, *T.B. Croat 23707* (K, L, NY, US); Vaca Plateau, 3 Aug. 1980, *C. Whitefoord 2024* (BM, MO, NY); South of Guacamallo Bridge, 10 May 1981, *C. Whitefoord 2826* (MO); Vaca Plateau, comune Ridge, 16°50'N, 89°06'W, 8 Aug. 1989, *M.J. Balick 2053* (MO, US); Cayo, Chial Road, 17°06'N, 89°06'W, 16 Feb. 1993, *R. Arvigo 737* (MO, NY); Mountain Pine Ridge, 8 Feb. 1994, *A. Monro & al. 153* (BM, MO); Chiquibul, San Pastor, 5 May 1995, *A. Monro 1018* (BM); Chiquibul Forest Reserve, track to Monkey Tail Branch, 10 Apr. 1998, *C. Whitefoord 10212* (BM, MO); **Corozal**. Port Sal, Aug. 1933, *P.H. Gentle 4905* (MO, NY, US); **Orange Walk.** Mile 54, Northern Highway, 25 Jan. 1974, *J.D. Dwyer & R. Liesner 12209* (K, L, MO, NY, US); **Stann Creek**. Middlesex, 14 Sep. 1929, *W.A. Schipp 332* (BM, G, MO, NY, US); Stann Creek-Sittee Road, 13 Jul. 1953, *P.H. Gentle 7975* (NY, US); Stann Creek, 14 Jun. 1954, *P.H. Gentle 8215* (BM, NY, US); Stann Creek, Silkgrass Creek Area, 8 Jan. 1955, *P.H. Gentle 8523* (G, NY, US); Stann Creek, ca. 5 miles S of Lynam Ag. College, 15 m, 7 Jul. 1970, *D.L. Spellman 1598* (MO); **Toledo**. Monkey River, 6 Sep. 1941, *P.H. Gentle 3657* (MO, NY); Toledo, comune Ridge, near Jacinto Creek, 7 May 1946, *P.H. Gentle 5572* (MO, US); Chavarrias Road, Resemederes, across Columbia River, 10 Oct. 1947, *P.H. Gentle 6278* (G, US); Between Macaca and Camp 2, 13 Dec. 1949, *P.H. Gentle 6931* (NY, US); El Dorado Road, 24 Jan. 1950, *P.H. Gentle 6963* (G, NY, US); Near San Antonio, 11 Oct. 1952, *P.H. Gentle 7785* (NY, US); NW of Punta Gorda on Owen Lewis private lane, 1 Aug. 1970, *J.R. Wiley 23* (M); Columbia Forest Station, 26 Jun. 1972, *J.D. Dwyer 9957* (MO); San Lose, 6.7 miles north of Columbia Forest Station, 13 Jun. 1973, *J.D. Dwyer 11155* (K, L, MO, NY, US); Vicinity of San Jose, Myan Indian Villane, 6.7 miles north of Columbia Forest Station, disturbed forest, 13 Jun. 1973, *T.B. Croat 24420* (K, L, US); Punta Gorda, 29 Jul. 1979, *J.D. Dwyer 14899* (BM, MO); Punta Gorda, 31 Jul. 1980, *J.D. Dwyer 15136* (BM, MO); Columbia Forest Reserve, 2 Oct. 1992, *C. Whitefoord 8269* (BM).

CAYMAN ISLANDS. Grand Cayman, 2 mi SE of Georgetown, 22 Jul. 1938, *W. Kings 166* (BM, NY); Grand Cayman, Governor's Creek Lagon, W. Bay, 29 May 1967, *M. Brunt 2031* (BM); Grand Cayman, N of Old Isaacs, 13 Jun. 1967, *M. Brunt 2191* (BM); Grand Cayman, North Side, along a graded road going inland through mangrove from the Queen's Highway just E of Old Man Bay, 11 Jun. 1998, *G.F. Guala II & al. 1901* (FTG, K, US).

COSTA RICA. Costa Rica, 1845-1848, *A.S. Ørsted 14127, 14128, 14130* (C); **Alajuela**. Vicinity of Los Chiles, Río Frio, 1 Aug. 1949, *R.W. Holm & al. 728* (BM); **Guanacaste**. Canton de La Cruz, da Bahia Salinas a Santa Cecilia, La Cruz, Santa Cecilia Hacienda El Oro, 500 m, 10°59'26"N, 85°25'40"W, 4 Sep. 1992, *R. Espinoza 528* (MO); Canton de Nicoya, Cuenca del Tempisque, sendero a las Cavernas, 10°09'52"N, 85°21'45"W, 2 Nov. 1996, *U. Chavarria 1627* (NY); La Cruz, along unnamed tributary of Quebrada Los Chanchos (between Quebrada Grande and Quebrada Los Chanchos), N slope of Cerros Santa Elena, Peninsula de Santa Elena, 100-200 m, 10.55N, 085.30W, 27 Jan. 2003, *M. Grayum & al. 11530* (USJ); **Limón**. 5 Jul. 1966, *R.W. Pohl & C. Calderón 9991* (MO, USJ); **San José.** Entre San Josè et le Capote, Jun. 1896, *A. Tonduz 7234a* (K); **Talamanca**. Foréts de Tráki, Apr. 1895, *A. Tonduz 9492* (G).

CURAÇAO. Mt. Christoffel, 26 Dec. 1952, *A.L. Stoffers 1184* (L).

CUBA. Camaguey. Cayo palma, 12 Oct. 1909, *J.A. Shafer 2571* (BM, NY, US); Habana, 1 Jun. 1905, *C.F. Baker 5324* (W); Herradure, 15 Aug. 1907, *S.M. Tracy 9094* (G, US, W); La Colombia near Havana, Nov. 1908, *Bro. León 767* (US); Jatovieja, Cayo Sabinal, 25 Mar. 1909, *J.A. Shafer 1073* (US); **Habana**. 1828, *Ramon de la Sagra 16* (FI-Webb); La Habana, prés Mariano, 2 Nov. 1908, *P. Levy s.n.* (L); Habana, Jamaica, 27 Jun. 1911, *Bro. León 2602* (US); Habana, Anafe, Laguna de Ariguanabo, 20 May 1914, *E.L. Ekman 1020* (NY); Habana, Cerro de Espeon, 7 Dec. 1930, *E.P. Killip 13509* (US); Habana, Valley of Yumutí river, Baracca, Aug. 1939, *Bros. León & M. Victorin 17336* (US); Habana, in swamp 2 km N of Nueva Gerona, Isla de Pinos, near sea level, 6-10 Feb. 1956, *C.V. Morton 9972* (US); **Las Villas**. Las Villas, 23 Jun. 1920, *Bro. Fernando Ansovin 349* (US); Las Villas, (Santa Clara), Sierra de San Juan, above San Blas, 300-600 m, 9-10 Nov. 1941, *C.V. Morton 4143, 4528* (US); ¼ mile west of Río San Juan crossing of road to Trinidad, 1-20 Jul. 1950, *R.A. Howard & al. 384* (K, NY, US); Sancti Spiritus, Banao, Loma de Banao, Tetas de Juana, 21°.876111N, 79°608888W, 600-840 m, 15 Mar. 2003, *J. Pipoly 24820* (FTG); **Mantanzas**. Woods near San Miguel, 7 Sep. 1903, *N.L. Britton & P. Wilson 241* (NY); Mantanzas, Cienaga de Zapata, Santo Tomas, 22°.422916N, 81°.1118W, 20 m, 13 Mar. 2003, *J. Pipoly 24740* (FTG); **Nueva Gerona**. Isle of Pines, Sierra de los Caballos, 2 Mar. 1916, *N.L. Britton & P. Wilson 15134* (NY); **Oriente**. Oriente, 1856-57, *C. Wright 747* (G, K, MO, NY, P, US, W), *C. Wright 748* (G, MO, NY, P, US); Santiago, vicinity of Baracoa, 24-29 Jan. 1902, *C.L. Pollard & al. 76* (MO, US); Santiago, Mar. 1903, *L.M. Underwood & F.S. Earle 1642* (NY); Oriente, Sierra Nipe, near Woodfred, 5 Dec. 1909, *J.A. Shafer 3017* (NY, US); Oriente, Gorge of the Río Yamuri, 7-9 Dec. 1910, *J.A. Shafer 7827* (NY, US); Oriente, Farallon de La Perla, 14 Feb. 1911, *J.A. Shafer 8751* (NY, US); Oriente, Bayate, 3 Jul. 1914, *E.L. Ekman 1723* (G); Oriente, Bayate, 1 Jun. 1915, *E.L. Ekman 5845* (K); North slope of Sierra Nipe, 400 m, 15 Oct. 1941, *C.V. Morton & J. Acuna 2914* (K, MO, NY, US); Northern spur of Sierra Maestra west of Río Yao, 24-30 Oct. 1941, *C.V. Morton & J. Acuna 3433* (K, NY, US); Renté, Santiago Bay, coastal thickets, Jun. 1943, *Bro. Clemente 2879* (US); Oriente, Moa Region, 8 km S of Moa, in "Cayo Chiquita", a pocket of moist hardwood forest in a valley surrounded by pinelands, 20°38'N, 74°57'W, 19 Jul. 1951, *G.L. Webster 3832* (NY, US); Santiago Region, dense scrub on limestone ca. 3 km N of El Morro, common, sprawling in shrubbery, 12 Aug. 1951, *G.L. Webster 4058* (US); Oriente, Crucero Dorales, Holguín Road to Tunas, 26 Dec. 1954, *M. Díaz-Piferrer s.n.* (FTG); Oriente, Cayo del Rey, SW base of the Sierra de Nipe, 100 m, 7 Jan. 1956, *C.V. Morton & al. 8753* (US); Oriente, Punton de Cuero, a mountain N of Imias, Southern coast of Oriente, 100-600 m, 11 Jan. 1956, *C.V. Morton & Bro. Alain 8879* (US); Holguin, near the Airport, Charrasco vegetation on limestone over serpentine, 100 m, 20°50'N, 76°20'W, 13 Jul. 1985, *A. Gentry 51046* (MO); **Pinar del Río**. Vicinity of Mendoza, 29 Nov. 1911, *J.A. Shafer* 10597 (MO, NY); Sierra de Anafe, 16 Dec. 1911, *P. Wilson 11363* (US); Arroyo del Sumidero, Aug. 1912, *J.A. Shafer & Bro. León 13564* (BM, NY, US); La Finca Caiguanabo, Sierra La Giura, 4 Feb. 1917, *W. Palmer s.n.* (US); San Cristobal, Loma del Pimento, 29 Sep. 1920, *E.L. Ekman 11527* (US); Tres Marias hill, Rangel, Rosario Mts., Aug. 1926, *Bro. Léon 12777* (US); Sabana de Troncones, El Rosario, Jul. 1929, *Bro. Léon 14118* (US); La Palma, Sur de Cajalbana, entre Saua y El Cayo, a orilla del arroyo Las Vueltas, 28 Aug. 1993, *X. Londoño & al. 830* (US); Viñales, Sierra del Infierno, 22°.767667N, 83°.400833W, 8 Mar. 2003, *J. Pipoly 24616* (FTG); **Villa Clara**. La Magdalena, Cayamas, Oct. 1904, *C.F. Baker 2501* (W); Santa Clara, Lomas de Banao, Feb. 1920, *A. Luna 206* (NY); Santa Clara, Caunao River to Cienfuegos Bay, 22 Mar. 1926, *J.G. Jack 4380 (*BM, NY); Santa Clara, San José, Trinidad Mountains, 30 Jul. 1936, *L.B. Smith & al. 3269* (MO, US).

DOMINICAN REPUBLIC. **Altagracia**. 15.1 km from Punta Cana on the new road to Otra Banda, 18°34'N, 68°29'W, 14 May 1980, *M. Mejía & T. Zanoni 6348* (MA, MO, NY); Near Laguna Turey, just W of the Punta Cana Beach Resort, 18°30'N, 68°22'W, 21 Mar. 2001, *D. Goldman 1994* (US); **Barahona**. Prope Barahona, 1910, *Bro. M. Fuertes 130* (G, W); Rincon, 1911, *Bro. M. Fuertes 1276* (C, L, MO, US); Barahona, near sea level, 24 Jan. 1922, *W.L. Abbott 1542* (US); Yaroa, La Cabirma, 1 Nov. 1954, *J. de Jesus Jiménez 2764* (US); 12 km NNE of Polo, along road to Cabral, 16 Aug. 1970, *G. Davidse 2721* (MO, NY, US), **n = 18!** (Davidse 1978); Sierra Martin Garcia, 4.5 km al E de Las Salinas, 18°19'N, 71°10'W, 30 Oct. 1985, *R. Garcia & al. 569* (NY); **Baoruco**. Environs du Lac Enriquillo, Dec. 1952, *Humbert 27605* (P); Baoruco, Sierra de Neiba, Los Guineos on upper river Río Colorado, 630 m, 18°35'N, 71°11'W, 11 Aug. 1990, *S.A. Thompson 7798* (MO); **Cibao**. Jaiquí Picado, 20 miles W of Santiago, 27 Nov. 1969, *A.H. Liogier 17049* (NY, US); Santiago de Los Caballeros, en la ladera SE de la loma Diego de Ocampo, 1070 m, 18°34'32"N, 70°44'00"W, 14 Mar. 2000, *A. Veloz & M. de La Cruz 2097* (MO); **Dajabón**. Sobre Cerro Chacuey (Cordillera Central), 400-800 m, 19°27'N, 71°35'W, 27 Nov. 1984, *T. Zanoni & al. 32386* (MO); **Distrito Nacional**. Santo Domingo City, 9-10 Mar. 1913, *J.N. Rose & al. 3739* (US); Ciudad Trujillo, 17 Dec. 1945, *H.A. Allard 14126* (NY, US); Km 32 along the Santo Domingo-Santiago Highway, 130 m, 11 Aug. 1970, *G. Davidse 2619* (MO, US); **El Seibo**. Between Punta Jicaco and Punta Rey, E of Jovero, Seibo Province, 29 Nov. 1923, *W.L. Abbott 2859* (NY, US); Los Haitises, approx. 2 km al Oeste de la Caseta de Guardaparques en Monte Bonito (de Trepida Alta), Parque Nacional Los Haitises, 19°00'N, 69°31'W, 200-300 m, 7 Aug. 1985, *M. Mejia & al. 35528* (US); Arroyo de Agua, 11.7 km W of El Valle, 200 m, 18°58'N, 69°28'W, 14 Jun. 1988, *T.B. Croat 68495* (MO, NY); **Espaillat**. Llanura de Nagua, 7 km al E de Gaspar Hernande proximo a La Ermita, 20-30 m, 19°38'N, 70°15'W, 14 Oct. 1982, *M. Mejía & J. Pimentel 23704* (MO); **Independencia**. 3 km S of Angel Feliz, 905 m, 18°37'N, 71°46'W, 16 Oct. 1991, *S.A. Thompson 9777* (MO); **La Romana**. La Romana, Isla Catalina, SW of La Romana, 10-20 m, 18°16'N, 69°02'W, 15 Jul. 1981, *T. Zanoni & al. 15451* (FTG, MO, NY); **La Vega**. Jarabacoa, 15 Jun. 1963, *Bro. Basilio Augusto 1015* (NY); La Vega, 16 km N of Jarabacoa along Highway, 260 m, 12 Aug. 1970, *G. Davidse 2641* (MO, US); Vega, on the road, near Hotel Montaña, Jarabacoa, 11 Jul. 1971, *J. de Jesus Jiménez 5937* (US); Cordillera Central, Loma La Pina o Loma de La Monja, 2 km E de Jarabacoa en la carretera a La Vega y 12 km N a Loma Firme, 700 m, 19°13N, 70°40'W, 26 Aug. 1983, *T. Zanoni & al. 26883* (MO); Loma del Puerto, from La Vega to Jarabacoa, 31 Aug. 1968, *Bro. A.H. Liogier 12410* (US); **Macoris**. San Pedro de Macoris, Mar. 1913, *J.N. Rose & al. 4159* (US); San Pedro di Macoris, 18 Oct. 1946, *R.A. Howard 9503* (BM, NY, US); 1.5 km E of Juan Dolio, 18°26'N, 69°25'W, 20 Aug. 1981, *T. Zanoni & S. Peláez 16225* (FTG, MO, NY); San Pedro de Macoris, Rio Cumayasa, en la Boca de Cumayasa, 18°24'N, 69°06'W, 20 Jun. 1986, *J. Pimentel & R. Garcia 598* (NY); **Monseñor Nouel**. Loma Peguera, Bonao, 300-400 m, 8 Aug. 1970, *A.H. Liogier 17367* (US); **Morne Espagnol**. 15°31.60'N, 61°27.84'W, 16 Aug. 2002, *S. Zona 951* (NY); **Nacional**. Loma Sierra Prieta mountain, 18°39'N, 69°53'W, 13 Aug. 1980, *M. Mejía & T. Zanoni 7842* (MO, NY); Nacional, base and lower southern slope of Sierra Prieta, 13.7 km N of Villa Mella, 14 Dec. 1986, *R. Carter & R. Garcia 5325* (MO); **Pedernales**. About 10 miles NE of Cabo Rojo, Pedernales, 11 Nov. 1969, *A.H. Liogier 16944* (NY); **Peravia**. San José de Ocoa on road to Cruce de Ocoa, 18°27'N, 70°29'W, 350 m, 26 Jun. 1980, *M. Mejia & T. Zanoni 7041* (FTG); La Cienega, carretera de San José de Ocoa a Río Abajo, 18°34.5'N, 70°27'W, 650 m, 26 Dec. 1980, *M. Mejía & J. Pimentel 9974* (FTG); Arroyo Palma, cerca del poblado la Toronja, 6 km SW de San José de Ocoa en la carretera a El Pinar, 18°32'N, 70°32'W, 24 Sep. 1985, *T. Zanoni & al. 27454* (NY); **Puerto Plata**. Loma del Puerto, 18 Sep. 1969, *A.H. Liogier 15917* (NY, US); 9 km SW of Sabaneto de Yasica along road to Jamao, 60 m, 13 Aug. 1970, *G. Davidse 2674* (MO); Cofresí, Puerto Alta, 24-25 Feb. 1973, *A.H. Liogier 18839* (NY); Puerto Plata, Pico El Murazo, 910 m, 19°41'N, 70°57'W, 28 Nov. 1992, *S.A. Thompson 11378* (MO); **Samaná**. Vicinity of Sanchez, Samaná Peninsula, sea level to 300 m, 5 Dec. 1920, *W.L. Abbott 179* (US); Laguna, Loma Zaramagua, 14 May 1930, *E.L. Ekman 14971* (US); En el paso y en la cara al viento (N) de Loma Pan de Azucar, subiendo del poblado de la La Laguna, 19°17'N, 69°18'W, 18 Jul. 1984, *T. Zanoni & al. 31159* (MO, NY); **San Cristóbal**. Cordillera Central, Villa Altagracia, edge of woods, 19 Jan. 1929, *E.L. Ekman 11246* (K, US); San Cristobal, poblado rural de Hato Damas, 10 km al N de San Cristobal en carretera a La Represa, 18°28'N, 70°07'W, 26 Oct. 1989, *J. Pimentel 1182* (NY); **San Juan**. El Cercado, 31 Aug. 1946, *R.A. Howard 8672* (BM, C, FI, MO, NY, P); **Santiago**. In fruticetis ad "Lopez", 8 Jun. 1887, *H.F.A. von Eggers 2380* (NY, US, W); Santiago, 16 Apr. 1906, *C. Raunkiaer 951* (C); San José de las Matas, Prov. Santiago, Jicomé, 24 Dec. 1929, *E.J. Valeur s.n.* (G, NY).

EL SALVADOR. Ahuachapán. San Francisco Menedez, Hda. San Benito, about 50 m above Casco San Benito, 820 m, 13˚49'N, 89˚56'W, 11 Nov. 1991, *W. Berendsohn 1377* (MO); Pie de propiedad Los Arteaga, 500 m alt., 23 Jan. 1998, *E. Sandoval ES-01763* (K); San Francisco Menéndez, El Corozo, Mariposario, zona alta "Los Sánchez", 380 m alt., 12 Apr 2000, *J.M. Rosales 543* (K); **Cuscatlán**. Cojutepeque, a orillas de calle al Cerro de Las Pavas, 16 Jan. 1996, *R. Villacorta 2328* (K).

GUATEMALA. s. loco, s.d., *E. Ritter von Friedrichsthal 1539* (W); **Alta Verapaz**. Cubilquitz, Jul. 1900, *H. von Tuerckheim 7696* (US); Near Pancajché, 5 Apr. 1939, *P.C. Standley 70615* (US); Alta Verapaz, Teleman, Panzos, 75 m, 22 Sep. 1987, *H. Droege 428* (MO); **Izabal**. Vicinity of Escoba, on the bay opposite Puerto Barrios, 2 Jun. 1922, *P.C. Standley 24889* (US); Izabal, near Puerto Barrios, Apr. 25-May 6 1939, *P.C. Standley 72832* (US); Izabal, Cerro San Gil, 26-27 Dec. 1941, *J.A. Steyermark 41967* (US); Izabal, forest between Río Dulce and Modesto Méndez, 30 Dec. 1972, *L.O. Williams & al. 41822* (BM, MO); Izabal, ca. 7 miles S of Puerto Barrios, 22 Jul. 1977, *T.B. Croat 41779* (M); Izabal, a 2 km all'O de El Estor, 31 Aug. 1988, *E.M. Martinez S. 23363* (MO); **Petén**. El Paso, 27 Apr. 1932, *C.L. Lundell 1587* (US); Chicbul, La Libertad, 1 Jun. 1933, *C.L. Lundell 3548* (US); La Libertad and vicinity, Aug.-Nov. 1933, *M. Aguilar 19* (K, MO, US); Dolores, about 2 km E of Río Mopan trail, 12 Jun. 1961, *E. Contreras 2448* (US);

Between Santa Elena and San Francisco, 12 Nov. 1965, *A. Molina 15628* (US); La Cumbre, on Pusila Road, 3 Aug. 1969, *E. Contreras 8838* (MO, NY); Petén, Lake Yaxha, 17 Jun. 1973, *J.D. Dwyer 11239* (MO); La Cumbre, on Pusila Road, 31 Aug. 1976, *C.L. Lundell & E. Contreras 20292* (NY); Laguna Macanché, Flores, 181 m, 16°58'25"N, 89°37'23"W, 23 Oct. 2008, *J. Morales 4973* (M); **Quetzaltenango**. Mountains near Santa Maria, 25 Mar. 1932, *P. Weatherwax 180* (K); Quezaltenango, above Mujuliá, between San Martin Chile Verde and Colomba, 1800 n, 1 Feb. 1941, *P.C. Standley 85472* (US).

HAITI. L'Artibonite. Vicinity of St. Marc, near sea level, 25-28 Feb. 1920, *E.C. Leonard 2907* (NY, US); Vicinity of Klacroix, Section Dessalines, Dep. de L'Artibonite, 11 Dec. 1925, *E.C. Leonard 7910* (W); Vicinity of Ennery, Dep. de l'Artibonite, 19 Jan. 1926, *E.C. Leonard 9007* (US, W); **Gonave**. Vicinity of Anse Galette, Gonave Island, 4 Mar. 1920, *E.C. Leonard 3071, 3072* (US); Vicinity of Anse Galette, Gonave Island, 3-14 Mar. 1920, *E.C. Leonard 3081* (NY, US); **Môle-Saint-Nicolas**. Nord-Ouest, entre 4 y 10.4 km al oeste de Baie de Henne en la carretera a Bombardopolis, 19°40'N, 73°15'W, 11 Jun. 1985, *T. Zanoni & al. 35093* (NY, US); **Nord**. Bayeux, near Port Margot, 12 Aug. 1903, *G.V. Nash 362* (NY); Vicinity of St. Michel de l'Atalaye, 15 Nov. 1925, *E.C. Leonard 7011* (NY, US); Vicinity of St. Michael de l'Atalaye, Département du Nord, 350 m, 30 Nov. 1925, *E.C. Leonard 7605* (US); Vicinity of Marmelade, 800 m, 19 Dec. 1925, *E.C. Leonard 8249* (US); Vicinity of Plaisance, 27 Jan. 1926, *E.C. Leonard 9293* (BM); Grande Cayemite, 21 Aug. 1927, *W.J. Eyerdam 326* (MO, P, US); **Ouest.** Massif des Matheux, Thomazeau, Morne à Cabrits, 350 m alt., 3 Jul. 1927, *E.L. Ekman 8559* (C, G, K, US); Barassa, M. des C., 7 Sep. 1944, *L.R. Holdridge 1945* (BM, MO, NY, US); **Nord-Oueste**. Entre 4 y 10.4 km. al "oueste" de Baie de Henne en la Carretera a Bombardopolis, 19° 40? N, 73° 15' W, 380 m, 11 Jun. 1985, *T. Zanoni & al. 35093* (US). **Port au Prince**. Vicinity of Mision, Fonds Varettes, 17 Apr.-4 May 1920, *E.C. Leonard 3785* (BM, NY, US); Vicinity of Pétionville, 350 m, 21 Jun. 1920, *E.C. Leonard 4950* (US); Port au Prince, 30 May 1923, *A.S. Hitchcock 19888* (US); Pétionville, 2 Nov. 1924, *E.L. Ekman 2334* (US); Vicinity of La Vallée, Tortue Island, 28 Dec. 1928-9 Jan. 1929, *G.M. Leonard & E.C. Leonard 11235* (K, MO, US), *11692* (US, W); Between Port Margot and Azul du Nord, 13 Jun. 1941, *H.H. Bartlett 17404* (US); Northward from Morne Jeffrard (i.e., within Arrondissement de Jérémie), along the road from Les Cayes to Les Roseaux, 10 Jul. 1941, *H.H. Bartlett 17558* (K, US); **Port de Paix**. Vicinity of Port de Paix, Dec. 1923, *E.C. Leonard 11116* (BM, P, US); **Sud**. Cayaba to Moron southern peninsula (places on the road from Dame Marie to Jérémie), 8 May 1941, *H.H. Bartlett 17312* (NY, US); Bouzi, Dabon, 24 Jun. 1980, *C.H.L. Sastre & Y. Polynice 7036* (P); Changieux, 28 Jun. 1980, *C.H.L. Sastre & Y. Polynice 7157* (P); Bois Formon, 18°.3186N, 74°.0096 W, 1020-1025 m, 2 Dec. 2012, *B. Jestrow 2012-429* (FTG).

HONDURAS. **Atlantida**. Vicinity of Tela, at sea level, 14 Dec. 1927-15 Mar. 1928, *P.C. Standley 54545* (US); Roatán Island, Bay of Honduras, s.d, *G.F. Gaumer 129* (K); San Juan carib village W of Tela, 28 Jul. 1934, *T.G. Yuncker 4811* (BM, MO, NY, W); Isla de Roatán, north slope of the mountain, 30 Nov. 1969, *F.A. Barkley & E.D. Barkley 39669* (MO); Mountain Nombre de Dios, between Saladino and San Francisco, 26 Apr 1967, *A. Molina 20845* (NY, US); 17 km SSE of La Ceiba along Río Cangreal, 26 Jun. 1970, *G. Davidse & R.W. Pohl 2126* (NY, US); 28 km NE El Progresso by road, 24 Jun. 1970, *G. Davidse & R.W. Pohl 2174* (MO, NY, US); 33 km SE of Tela by road in Valley of Rion Lean, 26 Jun. 1970, *G. Davidse & R.W. Pohl 2189* (MO, NY, US); 17 km SSE of La Ceiba along Río Cangregal, 30 m, 26 Jun. 1970, *G. Davidse & R.W. Pohl 2196* (MO), ***n* = 18!** (Davidse 1978); Zacate de 3 m de altura, Orillas del Río Piedras Gordas, Tela, 15 Aug. 1981, *C. Alvarado 26* (MO); Southern boundary of Lancetilla Valley, on ridge separating Lancetilla watershed from the watershed edges to the South, around San Francisco, edges of disturbed primary forest, 380-420 m, 15°41'30"N, 87°28'00"W, 8 Nov. 1988, *J.M. McDougal & al. 3368* (MO); **Comayagua**. Near Siguatepeque, 7 May 1936, *T.G. Yuncker & al. 5651* (G, MO, NY, US); Comayagua, margin of forest, summit of range above El Achote above plains of Siguatepeque, 1700 m, 21 Jul. 1936, *T.G. Yuncker & al. 6012* (G, K, NY, US); Comayagua, San José de Comayagua, 30 Jun. 1970, *G. Davidse & R.W. Pohl 2226* (L, MO, NY, US); **Colón**. Capuchin site west, 15°57'30"N, 85°54'30"W, 14 Jan. 1981, *J. Saunders 881* (BM, MO, NY); **Copán**. 11 miles S of Chiquila on Hgw. from la Entrada to San Piedro Sula, 300 m, 2 Aug. 1977, *T.B. Croat 42537* (MO); **Morazán**. La Tigra, 20 km NE de Tegucigalpa, 28 Apr. 1984, *H. Lainez 173* (NY); Morazán, Alrededores Col. Kennedy, 30 Jan. 1985, *V.M. Figueroa 156* (NY); **Lempira**. Near Gracias, Montaña de Claque, 20 Sep. 1991, *M. Chorley 341* (BM); **Mosquitia**. Near village of Barra Platano (= Ras) at mouth of the Río Platano, 84°42'W, 15°53'N, 25 Nov. 1976, *P. Fryxell 2842* (NY); **Olancho**. Valle Catamas, 19 Nov. 1963, *A. Molina 13291* (BM, US); Olancho 3 km SW of Dulce Nombre de Culmi, 500 m alt., 23 Jul. 1970, *G. Davidse & R.W. Pohl 2440* (K, MO, NY, US).

JAMAICA. Jamaica, 1850, *R.C. Alexander s.n.* (K); **Clarendon**. Ramble, 3 miles S of Claremont, 14 Oct. 1912, *A.S. Hitchcock 9519* (US); Lower Clarendon, 7 Dec. 1917, *W. Harris 12740* (K, MO, NY, US); Pickham Woods near Upper Clarendon, 27 Dec. 1917, *W. Harris 12768* (K, MO, NY); Portland Parish, Rodney Hall, 1000 ft, 12 Sep. 1962, *C.D. Adams 11638* (MO); Clarendon, upper W slope of Crofts Mountain, 4 Oct. 1968, *G.R. Proctor 29244* (BM); Clarendon, ca. 1-2 miles NW of the Mason River Field Station and 4-5 miles NW of Kellits, border of St. Ann & Clarendon Parish, 30 Dec. 1979, *J. Pruski 1534* (MO, NY, US); **Manchester**. Mandeville and vicinity, 29 Aug. 1907, *N.L. Britton 946* (NY); Southern Manchester, New Forest, 8 Nov. 1912, *A.S. Hitchcock 9838* (US); Southern Manchester, 20 Nov. 1917, *W. Harris 12691* (BM, K, MO, NY, US); Parish Manchester, Marshall's Pan, 6 Jan. 1959, *Robertson s.n.* (K); **St. Andrew**. Kingston, above Constant Spring, 25 Sep. 1912, *A.S. Hitchcock 9264* (US), *9268* (L, US); Castleton, 4 Nov. 1912, *W. Harris 11297* (MO, P); Robertsfield, Blue Mountains, 3 Dec. 1912, *W. Harris 11490* (C, K, MO, NY, US), *11491* (K, MO, US); St. Andrew, 26 Dec. 1912, *W. Harris 11528, 11530* (US); Long Mountain, along road to Wareika, 8 Jul. 1954, *G.L. Webster 4998* (BM, US); Long Mountain, 9 Nov. 1957, *T.G. Yuncker 17332* (BM, G, MO, NY); St. Andrew Parish, Cooper's Hill in the Red Hill, NW of Kingston, 2300 ft, 7 Aug. 1963, *M.R. Crosby & W.R. Anderson 1099* (MO, NY); **St. Ann**. Upper slopes of Mount Diabolo, Jul. 1926, 500-800 m, *W.R. Maxon & E.P. Killip 473* (US); Near Brownstown, 18 Jan. 1938, *F.W. Hunnewell 15224* (NY); Parish St. Ann, 1,4 miles S of Ocho Ríos at end of Fern Gully, 130 m, 26 Nov. 1971, *G. Davidse & E. Convoy 3274* (MO, US); **St. Catherine**. Bog Walk to Spanish Town, 26 Sep. 1912, *A.S. Hitchcock 9304* (US); Edwarton to Moneague, 10 Oct. 1912, *A.S. Hitchcock 9149* (US); Hollymount and vicinity, 750-850 m, 24 Jul. 1924, *W.R. Maxon 10463* (US); St. Catherine, Río Cobre, below Bog Walk, 3 Aug. 1939, *Phillipson 594* (BM); St. Catherine, NE slope of Juan de Bolas, 29 Jul. 1952, *G.R. Proctor 7108* (NY, USJ); St. Catherine, Mt. Diablo, Blue Mountain, 2.5 miles S by road of Hollymount Road, 21 Aug. 1965, *H.A. Hespenheide 1409* (MO, NY, US); **St. Elizabeth**. St. Elizabeth, 7 Mar. 1917, *W.*

Harris 12512 (BM, K, MO, NY, US); Balaclava, 1928, *C.R. Orcutt 1488* (BM); **St. James**. Montego Bay, 24 Oct. 1912, *A.S. Hitchcock* 9687 (US); **St. Mary**. Troy, 6 Nov. 1912, *A.S. Hitchcock 9802* (US); **St. Thomas**. St. Thomas Parish, 2.3 miles NE of the Eleven Mile intersection along road to Llandewey, 25 Nov. 1971, *G. Davidse & E. Convoy 3258* (MO, NY, US), **n = 18!** (Davidse 1978); **Trelawny**. Leroy, 16 Oct. 1917, *W. Harris 12572* (K, MO, NY, US), *12597* (C, K, MO, NY, US); Trelawny, NW corner of the crossroads at Burnt Hill, 23 Nov. 1974, *José L. Vivaldi 338* (FTG); **Westmorland**. Savanna La Mar, 10 Nov. 1912, *A.S. Hitchcock 9881* (US); Glasgow near Leroy, 19 Oct. 1917, *W. Harris 12629* (K, MO, NY); Westmoreland, Blauwearie, 31 Oct. 1952, *G.R. Proctor 7315* (US).

LEEWARD ISLANDS. Antigua. s.d., *Nicholson 28* (K); Antigua, 4–16 Feb. 1913, *J.N. Rose & al. 3660* (US); Antigua, between Liberta & Falmouth, 10 Sep. 1931, *H.E. Box 64* (K, MO, NY); Antigua, Macarthy Valley, 20 Sep. 1931, *H.E. Box 91* (BM, K, US); **Guadeloupe**. Littoral sec et cultures Anse Bertrand, 28 Apr. 1937, *H. Stehle 2607* (US); Safaïa, 6 Jun. 1937, *A. Questel 4646* (P); Jarry, 6 Mar. 1938, *A. Questel 600* (P, US); Port Louis, 12 Mar. 1939, *A. Questel 4023* (US); Marie Galante, SW of St. Louis, 5 Dec. 1959, *G.R. Proctor 20298* (BM, US); Deshaies, le Dos d'Ane, 500 m, 23 Sep. 1974, *J. Jeremie 193* (P); Désiderable plateau, 9 Sept. 1981, *S. Barrier 2997* (P); **St. Barthélemy**. 5 Dec. 1938, *A. Questel 845* (P); Nevis, 31 Jan. 1932, *H.E. Box 172* (K, US); St. Barthélemy Island, 9 Nov. 1957, *C. Le Gallo 549* (K, NY); **St. Eustatius**. 1906, *I. Boldingh 990* (P); **St. Kitts**. 13 Oct. 1919, *A.S. Hitchcock 16354* (US).

MEXICO. Baja California. *León de la Luz 4070* (CAS) in Rebman et al. (2016); Baja California Sur, La Paz, Sierra del Novillo: approx. 15 miles southeast of La Paz & northeast of the jctn. of Highway 1 & Highway 19; In a canyon above Rancho Las Calabazas on the northeast side of the Sierra, 23.94732 -110.17519, 655 m, 22 Oct. 2014, *J. Rebman 29186* (SD); Baja California Sur, Sierra de La Luna, Sierra La Victoria, ca. Rancho Termopilas, 23.70027 -109.98113, 729 m, 29 Sep. 2015, *León de la Luz 12294* (SD); **Campeche**. About 1 mile E of Highway 180 on road to Halchahen, 12 Aug. 1979, *J. Utley & al. 6463* (BM); 15 km al NE de Chunchintok, camino Ramon Corona, 19°26'00"N, 89°29'50"W, 25 Sep. 1984, *J.J. Ortiz 559* (MO); Between Xpujil and Campeche, 14 Jul. 1977, *J.D. Dwyer 14522* (MO, NY); Calkmul, a 1 km al W de Plan de San Luis, sobre la carretera Escarcega-Chetumal, 18°31'44"N 89°34'15"W, 26 Nov. 1997, *E.M. Lira C. 604* (MO); Camino al Rancho San Pablito Nohan, cerca del km 98 de la carretera Ciudad del Carmen-Campeche, 21 Sep. 1987, *E. Cabrera 14477* (MO); Calakmul, a 12 km al W del ejido Plan de San Luis, 274 m, 18°31'46"N, 34°32'W, 20 Sep. 2002, *D. Alavarez 2040* (MO); **Chiapas**. Near the junction of the Río Perlas and Río Jataté at San Quintin and near Laguna Miramar, 200 m alt., 15 Mar. 1955, *E.R. Sohns 1590* (K, US); Ocosingo, near Rancho Mumuntil near Ocosingo, 10 Jan. 1968, *A.S. Ton 3475* (NY); 15 km WNW of Ocozocoautla, 15 Oct. 1972, *D.E. Breedlove 29030* (NY); 12 km N of Palenque along road to Catazaja, 8 Nov. 1980, *D.E. Breedlove 47298* (NY); SW of Palenque on road to Ocosingo along the Jol Uj'um, 9 Nov. 1981, *D.E. Breedlove 55240* (NY); 9–12 km S of Palenque on road to Ocosingo, 11 Nov. 1981, *D.E. Breedlove 55368* (NY); Ocosingo, 8 km SE of Santo Domingo on road to Bonampak, 520 m, 14 May 1982, *G. Davidse & al. 20461* (MO); Yajalon, Los Pinos, 30 Oct. 1982, *A. Mendez Ton 4943* (MO); Tenejapa, Río Seco Cruz Pilal, 900 m, 10 Nov. 1982, *A. Mendez Ton 5027* (MO); Santa Maria, Union Juarez, 24 Aug. 1985, *E. Ventura & E. Lopez 2300* (NY); Ocosingo, loc. a 2 km al SE de Nuevo Guerrero, camino a Boca Lacantum, 350 m, 30 Jan. 1986, *E. Martinez 16949* (MO); Al N de la Colonia Benito Juárez Miramar, 23 Aug. 1993, *A. Reyes-García & Sousa 2227* (MO, BM); Ocosingo, a 1.5 km de la entrada al camino de Nuevo Tumbala, 8 Mar. 2002, *G. Aguilar M. 34* (MO); Ocosingo, arroyo de Nuevo Guerrero, a 500 m del poblado, hacia el sur, 210 m, 16°58'59"N 91°17'04"W, 28 Jun. 2002, *G. Aguilar M. 1615* (MO); Ocosingo, a 2.5 km al N de Sam Javier, 425 m, 16°27'43"N, 91°14'26"W, 21 Dec. 2002, *G. Aguilar M. 4829* (MO); Ocosingo, a 0.25 km al W del poblado Petalsino, 195 m, 17°0'16"N, 91°18'W, 14 Jan. 2003, *G. Aguilar M. 4917* (MO); **Chihuahua**. Aug.–Nov. 1885, *E. Palmer 10* (G); **Colima**. Manzanillo, woods on low hill near the coast, 19 Sep. 1910, *A.S. Hitchcock 410* (C, K); Alzada, shady ravine, 21 Sep. 1910, *A.S. Hitchcock 411* (C, G, K); **Guerrero**. 20.1 km al E de Petlaltina, 68.1 km al E de Chilapa, camino a Tlapa Gro., 170 m, 14 Nov. 1982, *R. Torres C. 1915* (MO); **Oaxaca**. 5 miles N of Palomar (54 miles N of junction Highs. 185 and 190), along 185, 65 m, 2 Jul. 1977, *T.B. Croat 40006* (MO); Oaxaca, Arroyo Pita, 23 km al N de Lazaro Cardenas, brecha a Sta. Maria Chimalapa, 320 m, 14 Mar. 1983, *P. Tenorio L. 3483* (MO); Mixe, Rancho La Ardilla, 7 km al E de Totontepec, 18 Jul. 1986, *E. Ramirez G. 391* (MO); Tuxtepec, Ayotzintepec, banks of Río Soyolapan, 150 m, 17°42'N, 96°17'W, 25 Apr. 1986, *R.E. Gereau & G.J. Martin 1981* (MO); **Jalisco**. Tequila, Aug.–Sep. 1886, *E. Palmer 362* (G, MO, NY, UPS, US); **Orizaba**. Orizaba, Jun. 1909, *Bro. Arséne s.n.* (L); **Quintana Roo**. San Miguel, Cozumel Island, 6–8 Aug. 1932, *J.R. Swallen 2897* (US); 9 km al Norte de Puerto Morelos, 10 Feb. 1980, *O. Jéllez 1557* (MO, NY); 1 km al norte de Playa del Carmen, 9 Mar. 1980, O. *Jéllez 1799* (MO); 9 km al SW de Puerto Morelos, carretera a Villarta, 17 Oct. 1980, *Vargas 3746* (BM); Al sur de Puerto Morelos, rumbo a Punta Brava, 5 Nov. 1980, *E. Cabrera 57* (MO, NY); En km. 2 sobre la brecha a Vallarta, 7 Nov. 1980, *E. Cabrera 146* (MO, NY); Brecha a Chumpon, 40 km al N de F. Carrello Puerto, 8 Dec. 1980, *E. Cabrera 589* (BM); Sobre km 25 de la Brecha a Tomas Garrido, 10 Dec. 1980, *E. Cabrera 700* (MO); 2 km S of Akumal om Highway 307 (Cancún-Felipe Carrello Puerto), 6 May 1982, *G. Davidse & al. 20120* (BM, MO); San Felipe Balacar, 8 May 1982, *G. Davidse & al. 20211* (BM, MO); 48 km NE of Felipe Carrillo Puerto on Highway 307 to Cancun, 10 m, 19 May 1982, *G. Davidse & al. 20623* (MO); A 10 km al sur de Akumal, 25 Sep. 1982, *E. Cabrera 3607* (MO); A 16 km al S de la Terminal del Ferry, cerca de la entrada a Palancar, 22 Nov. 1985, *E. Cabrera 9781* (MO); 4 km al N de la zona hotelera de San Miguel de Cozumel, sobre el camino a la Isla de la Pasion, Isla de Cozumel, ecotono de selva y manglar, 14 Jan. 1987, *E. Cabrera 12984* (MO); Felipe Carrillo Puerto, 19°52'8"N, 88°3'55"W, Jul. 2001, *M.E. Correa 6* (MO); **San Luis Potosí**. Tamasopo, Sierra Madre Oriental, 8–9 Aug. 1934, *F.W. Pennell 18014* (US); San Luis Potosí, 2 miles E of Tamazunchale, on N side of river, 24 Jul. 1940, *C.L. Hitchcock & L.R. Stanford 7311* (US); Between Tamazunchale and Chapulhuacan, 20 Aug. 1943, *C.L. Lundell & A.A. Lundell 12405* (NY, US); 21.4 km W of Ciudad Valles on the road to Río Verde, 27 Oct. 1985, *B. Bartholomew 3524* (NY); Along Highway 80 W of Antiguo Morelos, 18.7 miles of Antiguo Morelos, then 7.2 km N on asphalt road to El Salto, vicinity of El Salto to cataracts near military encampment, 200 m, 22°35'N, 99°25'W, 13 Jan. 1987, *T.B. Croat & D.P. Hannon 63055* (MO); **Tabasco**. La Palma, Balancan, 1–6 Jun. 1939, *E. Matuda 3242* (US); Tabasco, Tenosique, 12 km de Arena de Hidalgo, 7 Oct. 1980, *C. Cowan 3223* (MO, NY); **Veracruz**. Córdoba, prés La Luz, 2 Aug. 1862, *E. Kerber 74* (K); Jacuapan, Nov. 1907, *C.A. Purpus 2905* (NY); Córdoba, 27 Aug. 1910, *A.S. Hitchcock 409* (BM, C, US); Vicinity of Río Tonto, Ejido de Almilinga, 6 km W of Campo Experimental de Hule El Palmar, Zongolica, 30 Jul. 1943, *J.V. Santos 2269* (NY, US); La Laja, 14 Nov. 1963, *McRee*

10956 (P); Ocotal Chico, 20 km al N de San Pedro Soteapan, 700 m, 26 Jul. 1973, *G. Guevara 41* (MO); Brecha Hnos. Cedilo-La Escuadra-Hidalgotitlan, 6 May 1974, *B. Vasquez 608* (BM, MO); 6 miles of Coatzacoalcos along Highway 180, 3 Jul. 1977, *T.B. Croat 40038* (MO); Papantla, Cerro del carbon, 200 m, 9 Oct. 1982, *M.E. Cortes 472* (MO); **Yucatán**. s.d., *G.F. Gaumer 1032 pro parte* (MA, K, MO, US); Chichen, Itzá, 7-13 Jul. 1932, *J.R. Swallen 2452* (US), *2465,* (K, MO, US), *2469* (US); Tizimin, 14-16 Jul. 1932, *J.R. Swallen 2489* (US); Uxmal, 20-21 Jul. 1932, *J.R. Swallen 2512, 2625, 2641* (US); Peto, 26-27 Jul. 1932, *J.R. Swallen 2706* (US); 13 km W of Muna along road between Muna, Opichen & Maxcanu, 11 Aug. 1979, *J. Utley & al. 6424* (MO); Merida, ca. 12 km N of Merida, along Highway 273 to El Progreso, at Dzibilchaltun archeological site, 10 m, 20 Oct. 1984, *G. Davidse & J. Davidse 29441* (M); A 2 km all'O de Tahmek, sobre la carretera Valladolid-Merida, 29 Jun. 1985, *E. Cabrera 8784* (MO); A 17 km al E de Celestun, sobre la carretera Merida-Celestum, 20 Jul. 1985, *E. Cabrera 9056* (MO); A 10 km all'O de Chemax, sobre la carretera Cancun-Valladolid, 24 Sep. 1985, *E. Cabrera 9290* (MO); A 10 km al NO de Muna, sobre al cammino a Maxcanu, 30 Sep. 1985, *E. Cabrera 9581* (MO); Yucatán, 3 km al W de Koncal, 21°06'N, 89°42'W, 16 Oct. 1993, *L. Rico 1177a* (MO); 11 km al sur de la frontera Yucatán-Campeche, ca. de San Antonio Yax-ché, 20°05'00"N, 89°43'50"W, 20 Sep. 1999, *G. Carnevali & al. 5656* (NY); Santa Elena, zona Arqueologica de Sayil (Ruta Puc), 50 m, 20˚10'37"N, 89˚39'09"W, 21 Nov. 2006, *R. Duno de Stefano & G. Carnevali 2170* (MO); Tizimín, E del puerto El Cuyo, 21°30'51"N, 87°39'39"W, 22 Sep. 2011, *M.F. Cervantes & al. 825* (G).

NICARAGUA. **Río San Juan**. Carretera a San Miguelito, entre Río Oyate y San Miguelito, 100 m, 9-10 Feb. 1984, *A. Grijalva & N. Almanza 3597* (M); Río San Juan, Greytown, Caño Top House y el ultimo creek al a derecha viniendo a Greytown, Lagunas de San Juan Viejo, y en los alrededres de Greytown Nuevo, 11˚03'N, 83˚50'W, 6 Jan. 1995, *R. Rueda & al. 2608* (MO); **Zelaya**. Bilwascarma along Río Coco, 10 Jul. 1970, *G. Davidse & R.W. Pohl 2295* (MO, NY, US), ***n* = 18!** (Davidse 1978); Puerto Cabezas, 15 m, 14˚01'N, 83˚23'W, 3 Jul. 1980, *W.D. Stevens & al. 17811* (MO); Monkey Point, 3 km al S, 10 m, 11˚37'N, 83˚40'W, 24 Oct. 1981, *P.P. Moreno & J.C. Sandino 12276* (MO); Siuna, Wany, 27 Aug. 1982, *F. Ortiz 20* (MO).

PANAMÁ. **Bocas del Toro**. Isla Colón, NW side of Island, Mimitimbi Bluff, 31 Jan. 1989, *P.M. Peterson 6517* (MO, US). **Colón**. 0.7 miles NE of Río Piedras bridge on road from Pilón to Portobelo, 15 Mar. 1971, *M. Nee & S. Mori 3649* (MO, PMA); **Panamá**. Research Forest Site at Albrook Air Force Base, 22 Jun. 1967, *W.R. Stimson 5188* (NY, SCZ); Cerro Jefe, 09°14'N, 79°23'W, 7 Apr. 2002, *J.G. Sánchez-Ken 672* (US).

PUERTO RICO. s.d., *F. Riedle s.n.* (FI-Webb); Mayagüez, 22 Oct. 1884, *P.E.E. Sintenis 68* (G, K, W); Cayey, 20 Sep. 1885, *P.E.E. Sintenis 2470* (W); Cayey, ad rivulum Morillos, 5 Oct. 1885, *P.E.E. Sintenis 2318* (G, NY); Aguadilla, 1891-92, *Warning s.n.* (C); Río Piedrao, 22 Jun. 1901, *L.M. Underwood & R.F. Griggs 252* (US); Vicinity of Mayagüez, Monte Mesa, 17 Oct. 1913, *A. Chase 6157* (NY, W); Vicinity of Maricao, jungle bank of Río Maricao, 20-23 Oct. 1913, *A. Chase 6192* (L, NY, US); Vicinity of Vega Baja, 7 Nov. 1913, *A. Chase 6431* (US); Guanica Bay, 14-16 Nov. 1913, *A. Chase 6521* (US); Vicinity of Lares, 23 Nov. 1913, *A. Chase 6587* (US); Island of Vieques, north coast, 28-29 Nov. 1913, *A. Chase 6683* (US); Above Río Grande, Sierra de Luquillo, 1 Dec. 1913, *A. Chase 6726* (L, US); Vicinity of San Juan, Lake Loisa, 9 Dec. 1913, *A. Chase 6782* (US); Vicinity of Mayagüez, Monte Mesa, 12 Dec. 1913, *A. Chase 6814* (US); Vieques Island, 28 Jan. 1914, *J.A. Shafer 2549* (NY); Vicinity of Guancia, 5-8 Mar. 1915, *N.L. Britton & al. 4955* (NY); San Juan, Arecibo Road, 13 Jan. 1935, *C. Sargent 295* (BM, MO); Bayamon, Río Pedras, Station Grounds, 8 Nov. 1937, *J.I. Otero 255* (MO, US); Lavea, 24 Oct. 1943, *C. Sargent 3236* (K, MO); Mona Island, 9 Mar. 1944, *C.E. Chardon & J.I. Otero 811* (NY); Guayanilla, 18 Sep. 1959, *R. Woodbury s.n.* (US); Susua, 11 Jul. 1963, *A.H. Liogier 9899* (K, P); Rincon, road 115 between Rincon and Aquada just few miles N of Rincon, 2 Jul. 1966, *W.R. Stimson 3193* (MO); Culebrita Island, Nov. 1970, *R.O. Woodbury s.n.* (MO); Reserva Forestal Maricao, 760 m, 18°08'N, 66°58'W, 28 Dec. 1980, *J.C. Solomon 5714* (MO); Arecibo, Garrochales, Cambalache Commonwealth Forest, 18°26'57"N, 66°36'10"W, 50 m, 8 Dec. 1984, *D.K. Edelman 02* (US); Guanica Forest, 18°00'N, 66°50'W, 6 Jan. 1987, *B.M. Boom 6975* (MO); Salinas, Barrio Lapa, W peak Las Tetas de Cayey, 25 Oct. 1987, *P.M. McKenzie 781* (NY); Cayey-Salinas, base of towers on Cerro Las Tetas, 4 Aug. 1988, *C.M. Taylor 8138* (MO, P); Loiza, Calle Villanueva of Pueblo Indio, 13 Oct. 1989, *C.M. Taylor & al. 9481* (NY); Yauco, at end of route 333 in Guanica Reserve, from Playa Tamarindo along trail to cave, 0-30 m, 21 Oct. 1989, *C.M. Taylor 9508* (MO); Isabella, Bo. Arenales Alto, 30 Sep. 1990, *F. Axelrod & al. 1374* (NY, P); Cayey, Sierra de Jajome, 4 Nov. 1990, *F. Axelrod & al. 1583* (NY, P); Cayey, just W of the intersection of routes 184 and 179, private road along ridge leading to Barrio Farrallon, 18°07'N, 66°03'W, 9 Feb. 1991, *J.S. Miller & C.M. Taylor 5998* (MO); Guánica Forest Reserve (Manglillo section), headland at SW end of jeep road, dry scrub forest, 19 Nov. 1991, *F. Axelrod & P. Chavez 3296* (NY); Cabo Rojo, Sierra Bermela upper slopes and summit of Cerro Mariquita, 21 Dec. 1991, *F. Axelrod 3457* (NY); Montanas Aymamon, Reserva Forestal Guajatacas, ca. 10 km N of San Sabastian, Juan Perez Trail and Trail 4, 300 m, 17 Jan. 1992, *R.W. Sanders 1881* (MO); Quebradillas, Guajataca Forest, along trail Juan Perez, 28 Aug. 1992, *P. Acevedo-Rodriguez & D. Chinea 5218* (FTG, NY); Guanica Dry Forest Reserve, about 5 km by air E of Guanica, 17° 58'N, 66° 52'W, 15 Jan. 1992, *R.W. Sanders 1851* (FTG); Montañas Aymamon Reserva Forestal Guajatacas, ca. 10 km N of San Sabastian, Juan Perez Trail and Trail 4, 18°23'N, 67°01'W, 17 Jan. 1992, *R.W. Sanders & al. 1881* (FTG); Yauco, Susua Forest Reserve, along trail up slope E of Río Loco across from reserve office, 150-300 m, 15 Nov. 1992, *F. Axelrod 5364* (MO); Fajardo, Playa Convento, 18°22.778'N, 65°38.595'W, 19 Dec. 1994, *P. Acevedo-Rodriguez & A. Siaca 6984* (NY, US); Maricao, Río Maricao, 18°09'34"N, 66°59'53"W, 11 Feb. 1995, *J.A. Cedeno & Y. Jimenez 438* (NY); Guanica Forest Reserve, 6 Sep. 2000, *P. Acevedo-Rodriguez 11429* (NY); Guancia Forest Reserve, Canon de las Trichillias, from road 334 taking Las Cobanas Trail to the North, at the junction with other trail taking the drainage to the north, 17°59'09"N, 66°51'60"W, 110 m, 11 Nov. 2004, *O. Monsegur 253* (US).

USA (**Florida**). **Brevard Co**. Hummock, 30 Oct. 1902, *A. Fredgolm 5532* (K, NY, US); Dade Co., snapper hammock, 16 Nov. 1903, *A.A. Eaton 315* (K, US); **Collier Co**. Pinecrest, S of Tamiami Trail between Mile 40 and ochopee, 15 Apr. 1952, *H. Field & Y. Lazar s.n.* (US); Ca. 1 mi. near Paolita Station, 21 Sep. 1965, *D.B. Ward 5345* (BM, NY, US); Lee Co. Western Sanibel, 7 Jan. 1975, *W.C. Brumbach 8732* (NY, US); **Dade Co**. Biscagne Bay, 1874, *E. Palmer 630* (MO); Miami, Oct. 27-Nov. 13 1901, *J.K. Small & G.V. Nash 64* (US); Oak Hammock, 1906, *H.C. Cowles 012-2* (G, NY); Miami, 21 Dec. 1904, *S.M. Tracy 9320* (G, K, MO, NY, W); Miami, 9 Apr. 1906, *A.S. Hitchcock 723* (US); Elliott's Key, 19 Oct. 1906, *S.M. Tracy 9050* (G, MO, W); Hammocks, Long Key, (Everglades), 12-13 Jan. 1916, *J.K. Small 7345* (BR, C, NY, W); Between Miami and Cocoanut Grove, Nov.-Dec. 1913, *J.K. Small & G.K. Small*

4647 (G, NY, US); Royal Palm Hammock, 22 May 1925, *E.J. Palmer 27483* (MO); In everglades, along Tamismi Trail, 25 miles W of Miami, 26 Dec. 1927, *H.N. Moldenke 3747* (NY); Brickell Hammock, 17 Oct. 1933, *F. Duckett 212* (NY, P, UPS, US); Near Miami, 19 Jul. 1936, *D.S. Correll 5974* (US); Climbing on shrubs and low trees in palmetto-pine thicket on Big Pine Key, 11 Feb. 1966, *M.L. Smith 753* (VPI); Everglades National Park, Mosier Hammock at Long Pine Key, 11 Nov. 1977, *D.F. Austin & S.K. Austin 6651* (FTG); Nixon-Lewis Hammock, W of Homestead, 26 Jun. 1987, *A. Herndon 1765* (FTG, NY); Tropical hard wood hammock, ca. 0,5 miles E of Old Cutler Rd., 3 air miles NE of Perrine, 25°37'26"N 80°18'30"W, 9 Sep. 1994, *S.L. Orzell & E.L. Bridges 23184* (FTG); Key Biscayne, Aug. 1997, *M. Manna 2* (FTG; Castellow Hammock Env. Educational Center, 25°33.660N, 80°26'.733W, 2 Nov. 1997, *K. Bradley #1141* (FTG); **Indian River Co**. Hickets in shelly soil, Indian River, Florida, Jul., *A.H. Curtis 3588* (BM, BR, G, K, MO, NY, P, US, W); **Martin Co**. In coastal hammock by Indian River, Sewall's Point, E of Stuart, 15 Oct. 1975, *R. Kral 57134* (MO, NY); Twin Rivers Park, 2 Nov. 2007, *J. Bradford #327* (FTG); **Monroe Co**. Stock Island, 16 May 1917, *F.W. Pennell 9621* (US); Hammock S of Fort Pierce, 10 May 1918, *J.K. Small 8771* (NY); Key West, Mar. 1842, *F. Rugel 111* (BM, MO, NY, US); In dense tropical hammock, north end of Key Largo, a half-climbing shrub about 5 feet tall, 12 Jan. 1930, *H.N. Moldenke 407* (K, P, MO, NY, US, W); Newport, Key Largo, 1898, *C.L. Pollard & al. 157* (BM, NY, US); Key Largo, near Planter, 10-12 Sep. 1907, *A. Chase 3930* (US); Vacca Keys, in hammock, 28-29 Jan. 1909, *J.K. Small & J.J. Carter 2864* (NY, US); Boca Chica Key, in hammocks, 27 Nov. 1912, *J.K. Small 3947* (NY Johnson Hammock, 20 Nov. 1933, *W.M. Buswell 11* (FTG); Key Vacca, 13 Feb. 1935, *J.R. Swallen 5200* (US); Near Flamingo, 17-18 Feb. 1935, *J.R. Swallen 5248* (US); Big Pine Key, hammock, 1-17 Feb. 1937, *E.P. Killip 32037* (US); Big Pine Key, 29 Jan. 1940, *R.F. Martin 1281* (NY, US); Key Largo, 11 Feb. 1940, *N. Hotchkiss 6460* (US); Big Pine Key, end of road through NW hammock at old indian mounds, infrequent, 28 Mar. 1950, *J.R. Swallen 10694* (K, MO, NY, US); Dense thicket on Stock Island about 3 miles E of Key West, 5 Aug. 1950, *R.L. Wilbur & G.L. Webster 2556* (G, NY, US); Big Pine Key, 9 Nov. 1952, *E.P. Killip 42259* (US); Big Pine Key, S end, 25 Jun. 1956, *G.K. Briziky & W.L. Stern 253* (NY, US); Monroe-Dade county line, T54s, R34E, 25 Jan. 1963, *D.B. Ward & D. Burch 3306* (US); Monroe-Dade Co. Line, Branching and vinelike, climbing over shrubs and trees along small road into Hammock #7, in swampy part of hammock, 23 Feb. 1967, *M.L. Smyth 888* (VPI); Marathon Key, low area over dolomite, hammock clearing, 17 Jan. 1973, *R. Kral 49192* (MO); Key Largo, towards N end of the Key, 25 Oct. 1973, *D.S. & H.B. Correll 40304* (FTG, MO); Big Pine Key, sandy clearings, 23 Aug. 1974, *R. Kral 53983* (MO); N of Key Largo, 29 Jun. 1975, *S.R. Hill 3294* (FTG); Key Largo, growing in forest shade of hard wood hammock near northern end of island, 17-21 Mar. 1977, *M.R. Palmer 3402* (US); Big Pine Key, SE point, 17 Mar. 1982, *S.R. Hill 10988* (MO, NY); N end of Big Pine Key, 15 Sep. 1982, *D.S.* & *H.B. Correll 54043* (FTG, NY); Big Pine Key, 4 Mar. 1985, *D. Russell 31* (VPI); Key West National Wildlife Refuge, The Marquesas, SW Key (east), ca. 20.5 miles w of Key West, 3 Apr. 1996, *G. Gann & K. Bradley 529* (FTG); **Palm Beach Co**. Dry woods near Palm Beach, 5 Sep. 1895, *A.H. Curtiss 5530* (BM, G, K, L, MO, NY, P, US); Palm Beach, hammocks, 28 Dec. 1896, *H. Webber 204* (MO); Palm Beach, in hammocks near the beach, 19 Nov. 1904, *J.K. Small 2133* (NY).

VIRGIN ISLANDS. St. Croix 1871, *H.F.A. von Eggers 10* (C); Prosperity Garden, 5 Jan. 1906, *C. Raunkiaer 642* (C, P); River Estate, 4 Oct. 1923, *J.B. Thompson 385* (G); St. Croix, 1 Feb. 1955, *F.W. Hunnewell 20116* (NY); Mahogany Road, above Frederiksted, 12 Jan. 1979, *F.R. Fosberg 58915* (FTG); **St. John**. Sussanaberg, 17 Jun. 1984, *S. Mori & al. 16579* (FTG, NY); Hillside above Cinnamon Bay on road to Herman Farm, 60-120 m, 8 Nov. 1984, *S. Mori & R. Woodbury 17004* (FTG, MO); Cruz Bay, on trail to Solomon Beach, 16 Jan. 1988, *P. Acevedo-Rodriguez & A. Reilly 2288* (NY); Reef Bay Quarter, along Bordeaux Road, 200 meters from Center Line Road, 6 Jan. 1991, *P. Acevedo-Rodriguez & A. Siaca 3795* (FTG, MO); **Tortola**. Tortola, 13 Oct. 1918, *W.C. Fishlock 240* (NY); Road to Sage Mountain, 420 m, 25 Feb. 1988, *P. Acevedo-Rodriguez 2681* (MO); **Virgin Gorda**. Virgin Gorda, 5 Jan. 1919, *W.C. Fishlock 140* (NY); Gorda Peak National Park, north side of Gorda Peak, 11 Nov. 1999, *P. Acevedo-Rodriguez 10931* (NY, US).

WINDWARD ISLANDS. Barbados. Bay Gulley, Nov. 1935, *Intosh 3* (K, P); St. Joseph Parish, in forest on the Hackelton Cliff, near Bathsheba, above Andromeda Gardens, 17 Mar. 1977, *F.W. Gould 15047* (MO); **Dominica**. Hills N of Prince Rupert Bay, West Cabri, 28 Mar. 1956, *A.C. Smith 10306* (NY, US); Layou River Valley, stream NE of Clarke Hall, 23 Apr. 1964, *Ernst 1156* (BM); Road through Hungry Hill to Morne Plaisance, 18 Oct. 1984, *C. Whitefoord 4486* (BM, US); Saint John Parish, 2.3 km N of Cabrits Road junction along the NS Douglas Bay Road, 10 Dec. 1993, *S.R. Hill 25372* (MO, NY); St. Andrew Parish, Hampstead Heights, 0.5 km N of Hampstead River bridge, 100 ft, 15°35'N, 61°22'W, 23 Feb. 1997, *S.R. Hill 28897* (MO); Morne des Fous: Petit Colubri Estate, 15°12'47.4"N, 61°20'07.5"W, 13 Aug. 2002, *S. Zona et al. 936* (FTG); **Grenada**. Near Victoria, 1957, *G.R. Proctor 17221* (BM); **Martinique**. Chemin de St. Pierre, Jan. 1854, *C. Belanger 70* (G), *782* (G); Martinique, 1868, *T. Husnot 93* (BM); Céron à Grand Rivière, 14 Sep. 1937, *H. Stehle 2086* (US); Pic Paradis–Ravine de la Loterie, 388 m, Lat. -63.050106, Long. 18.075888, 6 Nov. 2021, *B. Ferlay & al. 1620* (P); **Montserrat**. Garibaldi Hill, 29 Jan. 1907, *J.A Shafer 700* (NY, US); **St. Lucia**. Shores of Marigot Lagoon, west coast, 30-200 m, 21 Mar. 1956, *A.C. Smith 10200* (NY, US); **St. Martin**. 1906, *I. Boldingh 2645* (L); **St. Vincent**. Kingshill, 27 Nov. 1945, *P. Beard 611, 1370* (US); NW peninsula of Connuoan Island, Mar.-Apr. 1950, *R.A. Howard 11100* (US).

TOBAGO. Near Parlatuvier, 22 Oct. 1937, *N.Y. Sandwith 1884* (K); Above Speyside, 30 Mar. 1993, *Clement & Ryves 596* (BM).

(4b) ***Lasiacis divaricata*** (L.) Hitchc. var**. *leptostachya*** (Hitchc.) Davidse, Ann. Missouri Bot. Gard. 64: 375. 1977.

Bas.: *Lasiacis leptostachya* Hitchc., Contr. U.S. Natl. Herb. 22: 19. 1920.

Type: *Nicaragua, Jinotepe, 500 m, stout central canes, branches more or less whorled and slender, floral branches conspicuously flexuous, panicles all small, jungle, 7 November 1911, A.S. Hitchcock 8718* (holotype: US! [barcode US00134108]; isotype BAA (photo!) [barcode BAA00002173]).

Description

Perennials caespitose. *Culms* up to 4-5 m tall, erect at the base, and usually clambering into vegetation; *secondary branches* fascicled, and zigzag arranged; *internodes*

3-8(-9) mm thick, hollow to completely solid with pith, glabrous, often densely papillose to slightly pubescent, with hairs up to 2 mm long; *nodes* glabrous. *Leaf sheaths* glabrous, overlapping margin ciliate with hairs up to 2.8 mm long, auricular hairs up to 1.5 mm long; *collars* puberulent to pubescent; *ligules* 0.5-1.0 mm long, membranous, a ciliate rim with small hairs to 1.0-1.5 mm long; *blades* 4-10(-12) cm long, 0.5-1.5 cm wide, linear-lanceolate, glabrous, acuminate, base asymmetrical, glabrous, margin scabrid. *Panicles* 2-8(-12) cm long, with the base included in the sheath; *branches* glabrous, scabrous, appressed ascending. *Spikelets* 4.0-4.5 mm long; oblong; *lower glumes* 1.8-2.5 mm long, 1.2-1.5 mm wide, 7-12-veined; *upper glumes* 3.0-3.8 mm long, 1.6-2.0 mm wide, 9-12 -veined; *sterile floret* with a staminate flower, *lemmas* 9-11-veined, *paleas* subequal the length of the fertile floret (as in var. *divaricata*), *anthers* 2.0 mm long; *fertile florets* 3.5-4.0(-4.5) mm long, 1.5-2.0 mm wide, *anthers* ca. 2.5 mm long, whitish, *stigmas* white; *caryopses* 2.5 mm long, 1.5 mm wide. *Chromosome number*: unknown.

Vernacular names

Costa Rica, Guanacaste, "*carricillo*" *O. Jimenéz 378* (US); San José, "*cañuela trepadora*" *O. Jiménez 892* (US); **El Salvador**, San Salvador, "*carrizo montés*" *S. Calderón 508* (NY, US), "*zacate carrizo*" *P.C. Standley 19136* (US); **Nicaragua**: León, "*carrizo*" *A. Grijalva & al. 4185* (MO).

Distribution

Belize, Colombia, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Venezuela, Windwards Islands.

Distribution (bibliographic references)

Hitchcock (1920); Lindeman and Stoffers (1963) as *L. harrisii* Nash; Pinto-Escobar (1966) as *L. leptostachya* Hitchc.; Davidse (1977, 1978, 1994, 2001); Pohl (1980); Serna and López-Ferrari (2000); Morales (2003); Sutherland (2008); Bono (2010); Dávila et al. (2018); Sánchez-Ken (2019); Menjívar Cruz et al. (2021).

Ecology

Forests edges in secondary and disturbed vegetation. From sea level to 2000 m.

Phenology

October through June.

Remarks

Var. *leptostachya* differs from var. *divaricata* for its small, narrow, glabrous leaves and panicles mostly included in the upper sheaths with divaricate pedicels and spikelets densely arranged. *Lasiacis divaricata* var. *leptostachya* can be confused with *L. harrisii* (cfr. Lindeman and Stoffers 1963: 181).

Selected Specimens

BELIZE. **Toledo**. Maya Montains, Union Camp, 23 Mar. 1977, *Boutin 5132* (BM); Toledo, 11 May 1979, *C. Whitefoord 1660* (BM).

COLOMBIA. **Boyacá**. Cordillera Oriental, quebrada afluente del Río Cusiana, abajo de Corinto, 24 Jun. 1967, *M. Mejía & al. 2753* (MA); **Cundinamarca**. Fusagasugá, 18 Jun. 1952, *Køie 5237* (C).

COSTA RICA. Costa Rica, 1845-48, *A.S. Ørsted 14129* (C); **Alajuela**. Upala, Bijagua El Pilón, Cerro La Carmela, 7 Jul. 1988, *G. Herrera 2010* (BM); **Cartago**. Cartago, 17 Aug. 1967, *R.J. Taylor 4471* (NY); Cerro Tablazo, NW of Tablon, 20 Aug. 1982, *R.W. Pohl 14136* (K, NY); **Guanacaste**. Prés Nicoya, 15 Jan. 1900, *A. Tonduz 13748* (BM, G, US); Buena Vista, Febr. 1910, *O. Jimenéz 378* (US); Santa Rosa National Park, 10˚51'N, 85˚37'W, 20 Jan. 1978, *R. Liesner 4229* (MO); Santa Rosa National Park, 30 km NW of Liberia, 320 m, 10˚50'N, 85˚35'W, 3 Nov. 1982, *D.H. Janzen 12241A* (MO); Cantón de Nicoya, P.N. Barra Honda, Cuenca del Tempisque, sendero a las Cavernas, s.d., *U. Chavarria & al. 1627* (K); Sendero Natural, Sector Santa Rosa, 27 Jan. 1997, *D.H. Janzen s.n.* (MO); **Puntarenas**. Canton de Buenos Aires, Rey Curré, a orillas de Río Terraba, Vuelta Campana, ca. 3 km aguas arriba sobre el Río Campana, 300 m, 9˚00'05"N, 83˚15'35"W, 11 Nov. 1991, *R. Aguilar 1438* (MO); **San José**. Alto del Rodeo, 28 Dec. 1884, *H. Pittier 1615* (US, W); Llano Grande de Curiscal, Febr. 1913, *O. Jiménez 892* (US); 0.5 km SE of Barbacoas, 1100 m alt., 7 Nov. 1968, *R.W. Pohl & G. Davidse 11406* (K, US); Ridge between Río Virilla and Quebrada Micos, along road between Finca Micos and Llano Limon, 550-660 m, 9˚56'N, 84˚18'W, 16 Jan. 1986, *M.H. Grayum & al. 6078* (MO); Mora, Colón, 13 Dec. 2001, *J. Quesada 928* (K); Pérez Zeledón, Tinamaste, 1000 m, 09°17'40"N, 83° 46'00"W, 26 Mar. 1998, *A. Estrada 1502* (USJ).

EL SALVADOR. **Ahuachapán**. Vicinity of Ahuachapán, Jan. 1922, *P.C. Standley 19878* (MO, US); P.N. El Imposible, Transecto 3, San Benito, 12 Dec. 1989, *A. Sermeño 33* (MO); San Benito, 8 Nov. 1994, *Dávila 784* (K); Cabanas, near of Illobasco, 21 Jan. 1998, *G. Davidse & al. 37114* (MO), *37118* (BM); **San Salvador**. San Salvador, 1922, *S. Calderón 508* (NY, US); Vicinity of San Salvador, Dec. 1921-Jan.1922, *P.C. Standley 19136* (US); **Santa Ana**. Parque Nacional Montecristo, Cerro Miramundo, 4 Sep. 2002, *R.A. Carballo 484* (BM).

GUATEMALA. **Jutiapa**. Vicinity of Jutiapa, 24 Oct.-5 Nov. 1940, *P.C. Standley 75416* (US); **Mazatenango**. in dumetis, Nov. 1862, *G. Bernoulli 48* (G, K, NY, W); **Sacatepéquez**. Along Río Madre Vieja, above Patulul, 6 Jan. 1939, *P.C. Standley 62204* (US); Sacatepéquez, Volcán de Acatenango, 6 Oct. 1999, *M. Véliz 99.7712* (BM). **Santa Rosa**. region of La Sepultura, W of Chiquimulilla, 5 Dec. 1940, *P.C. Standley 79364* (US).

HONDURAS. **Camayagua**. La Chácara, 6 km N of Minas de Oro, 3 Aug. 1985, *Donaire 22* (BM); **Copán**. NE of Santa Rita de Copán, 28 Dec. 1973, *L.O. Williams & al. 42920* (BM); **Cortés**. El Cusuco, 20 km SW of San Pedro Sula, 1 Oct. 1989, *Galo 77* (BM); **El Paraiso**. 32 km W of Danli, 700 m, 19 Jun. 1970, *G. Davidse & R.W. Pohl 2145* (MO); 35 km NE of Chichicaste along Río Guayambre, 300 m alt., 31 Dec. 1978, *R.W. Pohl & M. Gabel 13834* (K, MO); **Yoro**. Río Pijol Valley, S of Nueva Esperanza, 28 May 1993, *R. Liesner 26611* (BM). **Huehuetenango.** Santa Barbara, between Zacapa and El Mochito, 600 m alt., 30 Dec. 1978, *R.W. Pohl & M. Gabel 13826* (K, MO); **La Paz**. Sobre el matorral del bosque mixto de Cordillera Guajiquiro, 5 km a Sabanetas, 21 May 1964, *A. Molina & A.R. Molina 13894* (US); **Morazán**. Montaña La Tigra, 35 km NE of Tegucigalpa, 10 Sep. 1989, *J.M. Perla 19* (BM).

MEXICO. **Chiapas**. 13 km N of Arriaga along Mexican Highway #195, 4 Oct. 1972, *D.E. Breedlove 28304* (NY); Chiapa de Corzo, 16.5 km NE of Chiapa de Corzo, 3 Nov. 1980, *P.A. Fryxell & E.J. Lott 3281* (NY); Cintalpa, 28 Jan. 1990, *A. Reyes García & al. 1491* (BM); La Concordia, 13 Jul. 1990, *A. Reyes García & R.J. Hampshire 1895* (BM); **Oaxaca**. 9 miles SE of Tapanatepec, 20 Oct. 1965, *D.E. Breedlove & P.H. Raven 13704* (NY); 1,5 miles E of Ayautla on road to Tuxtepec, 31 Jan. 1981, *J. Bauml & M. Kimnach 464* (US); San Miguel del Puerto, Pochutla, 610 m, 15°56'36"N, 96°5'43"W, 25 Nov. 1999, *J.F. Castrejon R. 925* (MO); **Veracruz**. Huitamalco, Jun. 1841, *F.M. Liebmann 6308* (C); Soteapan, Cerro Campanario, 14 Jul. 1987, *R. Acosta & L. Ceja 1668* (NY); San Martín, Veracruz, Nov. 1932, *H.W. von Rozynski 589* (MA).

NICARAGUA. **Boaco**. 24 Jan. 1970, *F.C. Seymour 3840* (BM, MO, NY); **Comalapa**. León, Hacienda La Pelona (El Provenir), Cerro La Pelona, a 2.5 km al NO de la Casa Hacienda, 500-600 m, 14 Dec. 1984, *A. Grijalva & al. 4185* (MO); **Río San Juan**. Greytown, 1867-68, *W.R. Tate 364* (K); **Madriz**. Lower W slope of Cerro Volcán de Somoto, 13°25'N, 86°35'W, 13 Dec. 1979, *W.D. Stevens & al. 16320* (BM, MO); **Jinotepe**. 3-7 Nov. 1911, *A.S. Hitchcock 8722, 8723* (NY, US).

PANAMA. **Colón**. Ca. 6 km N of Chilibre, along shores of Madden Lake (Lago Alajuela), 25-50 m, 9°12'N, 79°36'W, 26 Dec. 1981, *S. Knapp 2723* (MO, NY); Colón, La Pintada, Llano Grande, Finca Manuel Bern, 29 Jan. 2014, *O.O. Ortiz & R.M. Baldini 1982* (FT, PMA); **Panamá**. Canal Zone near Lhajuela, Chagres Valley, 12-15 May 1911, *H. Pittier 2342* (BM, NY, US); Canal Zone, between Madden Dam and Saddle 11 near Alahuela, 25 Nov. 1934, *C.W. Dodge & al. 16513* (MO, US); Canal Zone, Madden Lake, 20 Oct. 1975, *J.T. Witherspon & al. 8815* (MO); **Darién**. Darién, Camp Dubaganala, Helipad in Premontane Rain Forest, 15 Mar. 1968, *J.A. Duke 15495* (US); Majé, up Río Majé about 5 miles, steep forested ridge above Chocó Indian trail, 400 m, 18 Nov. 1970, *H. Kennedy & R. Foster 677* (MO).

VENEZUELA. Mérida. Tabay, 2 Sep. 1930, *W. Gehringer 398* (G); **Trujillo**. Alrededores de La Puerta, Valle del Río Momboy, 2000-2200 m, 11 Jan. 1982, *J. Bono 768* (FT).

WINDWARD ISLANDS. **Martinique**. Nov. 1867, *L. Hahn 480* (BM, FI, G, K, L, P, PI); Fort de France, Rivière Madame, 12 Jan. 1876, *C. Thiébaut* 371 (P).

(5) *Lasiacis grisebachii* (Nash) Hitchc., Bot. Gaz. (Crawfordsville) 54: 302. 1911. (Fig. 16).

Bas.: *Panicum grisebachii* Nash, Bull. Torrey Bot. Club 35: 301. 1908.

Type: *Cuba, vicinity of Madruga, coral rock ravine, 28 Mar. 1903, N.L. Britton, E.G. Britton & J.A. Shafer 758* (holotype: NY! [barcode NY00071078]; isotypes K! [barcode K000308104] as *Panicum martinicense* Griseb., US! Fragment from NY [barcode US00148550]).

(=) *Lasiacis grisebachii* (Nash) Hitchc. var. *lindelieana* Davidse, Ann. Missouri Bot. Gard. 64: 375. 1977.

Type: *Cuba, Habana, Lomas de Camoa, in sylvis locis umbrosis satis frequens, 27 Nov. 1921, Ekman 13530* (holotype: US! [barcode US00956494]; isotypes BM! [barcode BM000927718], F (photo!) [Acc. No. 1474168F], G! Two sheets [barcode G00176058, G00614201], L! [barcode L0797333], NY! Three sheets [barcode NY00888539, NY00888540, NY00888541], U (photo!) [barcode U0008351], US! Two sheets [barcode US00956495, US00956496], W! [Acc. No. W19590000023]).

(-) *Lasiacis rhizophora* Auct. Fl. Cub., non *L. rhizophora* (E.Fourn.) Hitchc.

Description

Perennials, caespitose. *Culms* 60-70 cm long, widely creeping and branching, distal ends of the branches erect, rooting at the lower nodes, forming prop roots 2-4 mm thick, branched above the soil, slender, apparently herbaceous to mildly lignified, usually forming a curled up network; *internodes* usually glabrous; *nodes* glabrous. *Leaf sheaths* puberulent, rarely hirsute, the overlapping margin weakly ciliate; *collars* with a line of hairs; *ligules* 0.3-0.5 mm long, membranous, inconspicuous, glabrous to weakly ciliolate; *blades* 5-15 cm long, 0.5-1.5(-2.0) cm wide, linear-lanceolate, acuminate, base usually asymmetrical, adaxial surface usually glabrous, rarely sparsely pubescent to glabrous, abaxial surface usually sparsely puberulent, rarely glabrous, margin scabrid. *Panicles* 4-12(-14) cm long, bearing only a few spikelets throughout. *Spikelets* 3-4 mm long, globose; *lower glumes* 1.5-2.5 mm long, 5-6-veined; *upper glumes* 2-3 mm long, 6-12-veined; *sterile florets* staminate with rudimentary or fully developed stamens, *lemmas* 7-12-veined, *paleas* subequal to the length of the fertile floret, margins enrolled; *fertile florets* 3-4(-4.5) mm long, 2-2.5 mm wide, *anthers* 2 mm long, white, *stigmas* white. *Chromosome number*: unknown.

Iconographs

Lámina 153 (Catasús Guerra 2012b).

Vernacular names

Cuba: "*alpiste cimarron*", "*cañutillo*", "*tibisi del monte*" (Roig 1963; Acevedo-Rodríguez and Strong 2012; Catasús Guerra 2012a).

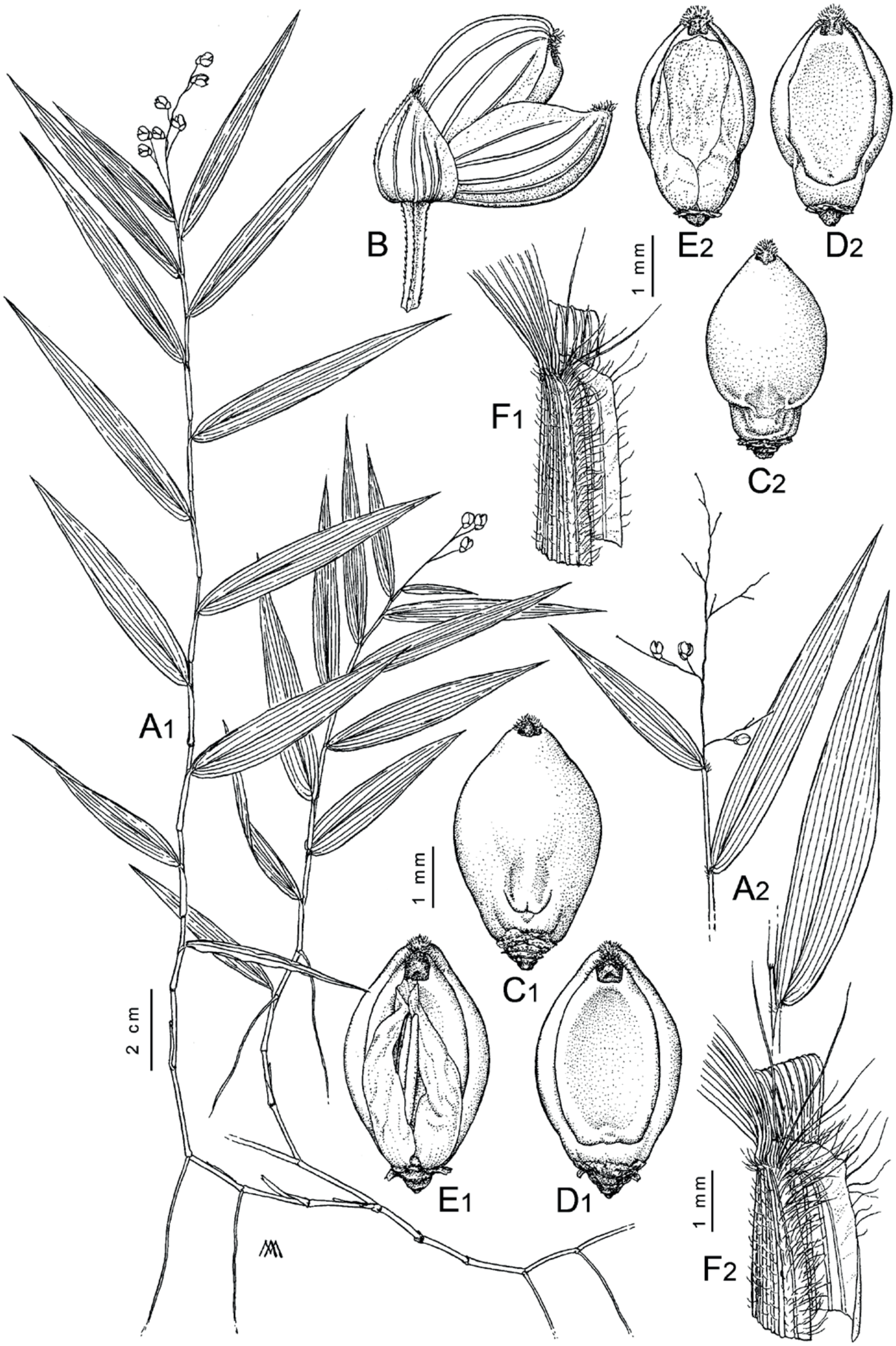

Figure 16. *Lasiacis grisebachii* (Nash) Hitchc.: **A1**. Habit, rooting at the nodes; **B**. Spikelet lateral view [A1-B. *L. grisebachii*, from *E.L. Ekman 1024* (L)]; **C1**. Fertile upper floret dorsal view; **D1**. Fertile upper floret ventral view without lower persistent palea; **E1**. Fertile upper floret ventral view with lower persistent palea; **F1**. Ligular area [C1-F1. *L. grisebachii*, from *E.L. Ekman 13531* (K)]; **A2**. Culm at the apex; **C2**. Fertile upper floret dorsal view; **D2**. Fertile upper floret ventral view without lower persistent palea; **E2.** Fertile upper floret ventral view with lower persistent palea; **F2**. Ligular area. [A2-F2. Cf. *var. lindelieana* Davidse from *E.L. Ekman 1023* (L)]. *A. Maury delineavit.*

Distribution

Belize, Costa Rica, Cuba, Guatemala, Honduras, Mexico, Nicaragua, Puerto Rico. (Fig. 17)

Distribution (bibliographic references)

Nash (1908) as *Panicum grisebachii* Nash; Hitchcock (1909) as *Panicum grisebachii* Nash (1913); Hitchcock and Chase (1917); Hitchcock (1911, 1913, 1920, 1930, 1936); Nash (1931); Swallen (1936, 1955b); Beetle (1977); Davidse (1978, 1994, 2001); Serna and López-Ferrari (2000); Zuloaga et al. (2003); Catasús-Guerra (2012a); Acevedo-Rodríguez and Strong (2012); Villaseñor (2016); Sylvester (2017); Dávila et al. (2018); Sanchéz-Ken (2019).

Ecology

Shade, usually in secondary forests, and in undisturbed areas. From sea level to 900 m.

Phenology

June/July through April in Central America, October through February in Cuba.

Remarks

The holotype of *L. grisebachii* var. *lindeileana* Davidse in US [US00956494] bears 2 labels in E.L. Ekmann's handwriting (see also in Davidse 1978):

"*Lasiacis lindelieana Ekmann n. sp. Cuba, prov. Habana, Lomas de Camoa, in silva locis umbrosis satis frequens, 27 Feb. 1921, E.L. Ekmann. // Obs.1 Same bind of localities as L. grisebachii. To date .... from two localities only Río de Mosquitos in Prov. Pinar del Río and Lomas de Camoa near Habana. Obs.2 Dedicated to my friend Mr. A.N. Lindelie, from St. Petersburg, Fla., administrator of Pan Ramon near Mariel, where I have been living these last two years. Obs.3 Related to L. grisebachii but easily recognized on its broader smoother nearly gla-*

Figure 17. *Lasiacis grisebachii* (Nash) Hitchc.: general geographic distribution.

brous blades and more robust stature". Nash was convinced to propose a new species, but he never formally described it.

In Fig. 16 the comparison of the diagnostic characters between var. *grisebachii* and var. *lindeileana* Davidse are outlined, showing their inconsistency to justify even a difference at the varietal level. Due to its sympatric distribution (Cuba) and the overlap of some diagnostic characters (e.g., the panicles small and shortened to nearly elongate, the blade with the surface from sparsely pubescent to nearly glabrous, and the stature from creeping to suberect habit) of both varieties, we follow the treatment of Catasús Guerra (2012a). *Lasiacis grisebachii* var. *lindeileana* can often be confused with *L. ruscifolia* (Catasús Guerra 2012a).

Selected Specimens

BELIZE. Belize. Belize, 12 Sep. 1928, *Simpson 8* (K); Honey Camp, Oct. 1929, *C.L. Lundell 559, 559a* (K, MO, NY, US); Sibun River, Gracy Rock School, 28 Nov. 1968, *R.R. Innes 59* (K); Gracie Rock, 1.5-4 miles S of Mile 22 on Westerm Highway, 100 m, 21 Jan. 1974, *R. Liesner & J. Dwyer 1483* (MO); **Cayo**. Between El Cayo and Benque Viejo, 15 Feb. 1931, *H.H. Bartlett 11505* (US); El Cayo, San Augustin, mountain pine forest, Jul.-Aug. 1936, *C.L. Lundell 6751* (US); El Cayo, Cave Branch Section, Hummingbird Highway, 13 Sep. 1955, *P.H. Gentle 8864* (NY, US); 41 miles Section, Belize-Cayo Road, 23 Feb. 1958, *P.H. Gentle 9641* (MO, NY, US); Milionario, 12 Dec. 1968, *G.R. Proctor 29866* (BM); Ca. 3 km S of Grano de Oro on road between Milionario and La Flor, 2 Jun. 1973, *T.B. Croat 23398* (K, MO); Vaca Plateau, 3 Aug. 1980, *C. Whitefoord 2025* (BM, MO, NY); Maya Mountains, Smokey Branch, 19 Mar. 1994, *A. Monro & al. 249* (BM); Chiquibul, Las Cuevas, 15 Mar. 1997, *A. Monro 1745* (BM); Chiquibul, Ceibo Grande to Main Divide track, 500 m, 16˚31'49"N, 89˚05'06"W, 26 Aug. 1998, *A.K. Monro & S. Cafferty 2684* (MO); Chiquibil Forest Reserve, Monkey Trail of Guacamallo river, growing on riverside, 16°44'N, 88°56'W, 3 Sep. 1998, *R.I. Vargas 96* (NY); Green Hills, 12 km on Chiquibil Road, 250 m, 17˚05'44"N, 88˚58'28"W, 25 Nov. 1998, *B.K. Holst & al.* 7135 (MO); **Orange Walk**. Río Bravo Conservation and management Area, 17˚49'N, 89˚02'W, 11-30 Oct. 1991, *N.V.L. Brokaw & M. Schulze 60* (MO); **Stann Creek**. Hummingbird Highway, 17 Sep. 1954, *P.H. Gentle 8384* (BM, NY, US), 11 Nov. 1954, *P.H. Gentle 8441* (US); Road E of Papal Volunteers House, Lynam Ag. College, 22 Mar. 1967, *J. Dwyer & al. 544* (MO); **Toledo**. Temash River, 3 Aug. 1935, *W.A. Schipp 1276* (BM, G, K, MO, NY), as *1376* (US); Río Grande, 4 Sep. 1944, *P.H. Gentle 4798* (MO); Mason's Land, 29 Sep. 1949, *P.H. Gentle 6849* (NY, US); Near Columbia, 2 Aug. 1950, *P.H. Gentle 7101* (G, US); Near San Antonio, 17 Nov. 1951, *P.H. Gentle 7523* (BM, C, G, NY, US); Southern Maya Mountains, Bladen Nature Reserve, 450 m, 16˚31'05"N 88˚54'11"W, 25 May 1996, *G. Davidse 36262* (MO); Bladen Nature Reserve, in the lowlands of the NE BNR, 45 m, 16˚33'N, 88˚43'W, 16 Feb. 1997, *S.W. Brewer 172* (MO); BFREE Reserve, Lagoon Trail, 45-75 m, 20 Oct. 2005, *C. Whitefoord & V. Queiroz 106019* (MO).

COSTA RICA. **Alajuela**.San Migiel de San Ramon, 11 Jan. 1937, *A.M. Brendes 21911* (NY); Alajuela, vicinity of Los Chiles, Río Frio, 11°02'N, 84°44'W, 1 Aug. 1949, *R.W. Holm & H.H. Iltis 728* (G, NY, UPS).

CUBA. Cienfuegos. Yaguaramas, savana de Alcade Mayor, 22°15'38.9"N, 80°39'54.9"W, 12 Dec. 2002, *E. Lewis & al. CEL 02-060* (FTG); **Habana**. Lomas de Camoa, 7 Nov. 1921, *E.L. Ekman 13462* (US); La Habana, Lomas de Camoa, 21 Nov. 1921, *E.L. Ekman 13511* (C, K, L, NY, P, W); La Habana, Lomas de Camoa, 27 Nov. 1921, *E.L. Ekman 13531* (K, NY, P, US); La Habana, Loma de Coco, Campo Florida, 27 Nov. 1921, *E.L. Ekman 1024* (C, FTG, G, K, L, NY, W); Habana, La Vigia, Tapaste, 2 Jan. 1922, *Bro. León 10666* (US); Habana, base of Pan de Cuajaibon, Las Pozas, Apr. 1952, *Bro. Alain 2415* (US); Habana, Managua, on a low hill, 15 Feb. 1956, *C.V. Morton 10198* (US); **Mantanzas**. 1849, *F. Rugel 187* (K, L, NY); Cuba, 1865, *C. Wright 3457 pro parte* (MO, NY, US); **Pinar del Río**. Mountains above Taco Taco, 28 Oct. 1909, *C.F. Baker 3817* (W); Trail from Buenaventura to San Juan de Guacamalla, 16 Dec. 1910, *P. Wilson 9332* (K, NY, US); Sierra de Anafe, 21 Dec. 1911, *P. Wilson & Bro. León 11467* (NY, US); Bahia Honda to El Rosario, 29 Jan. 1912, *J.A. Shafer 12006* (NY, US); Cabañas, towards Sierra de Las Animas, 15 Mar. 1920, *E.L. Ekman 10506* (G, K, NY, US); Gerardo, 18 Dec. 1920, *E.L. Ekman 12646* (US); Vinales, 11 Dec. 1930, *E.P. Killip 13528* (US); Source of Río, Taco-Taco, Sierra de Los Organos, 18 Nov. 1941, *C.V. Morton 4276* (US), *4306* (K, NY, US), *4390* (MO, US); **Villa Clara**. Santa Clara, Peninsula de Zapata, fores along the railroad from Central Australia to Bahia de Cochinas, 31 Jan. 1924, *E.L. Ekman 18340* (G, US).

GUATEMALA. **Izabal**. W of Santo Tomás de Castilla, near Guatel antennas on one of the summits of Cerro San Gíl, humid evergreen forest on slopes, 15°13'N, 88°59'W, 21 Sep. 1997, *M. Nee & al. 47330* (NY); **Petén**. Uaxactum, 19 Mar. 1931, *H.H. Bartlett 12190* (NY, US); Forest between Finca Yalpemech along Río San Diego and San Diego on Río Cancuen, 25 Mar. 1942, *J.A. Steyermark 45305* (US); Tikal, along Remate Road, 3 Jul. 1959, *C.L. Lundell 16144* (G); El Petén, San Luis, 11 Jul. 1959, *C.L. Lundell 16360* (G, US); Tikal, 23 Sep. 1959, *O. Degener 26713* (BM, NY); Tikal National Park, bordering Aguada Terminos, 30 Mar. 1960, *C.L. Lundell 16665* (US); About 6 km W of Dos Lagunas, on Carmelita Road, 6 Nov. 1960, *E. Contreras 1596* (M); Entre La Libertad y Subin, 50 km S de Sta. Elena, 10 Nov. 1965, *A. Molina 15503* (US); Sacate, 25 Sep. 1969, *R.T. Ortíz 326* (BM, MO, NY, US); **Quezaltenango**. Along old road between Finca Pirineos and Patzulin, 9 Feb. 1941, *P.C. Standley 86936* (US).

HONDURAS. **Lempira**. Guarunta, Wispernini Camp, Mar. 1938, *C. von Hagen & W. Von Hagen 1342* (NY); Punto Serra, 24 Jan. 1903, *P. Wilson 169* (NY, US); **Ocotepeque**. 18 km E of Nueva Ocotopeque, 15 Jul. 1971, *W.E. Harmon & J.A. Fuentes 6473* (NY); **Olancho**. 12 km SW of Dulce Nombre de Culmi along Highway 3, 23 Jul. 1970, *G. Davidse & R.W. Pohl 2442* (MO, NY, US); **Santa Barbara**. Between Lago Yojoa & El Sauce, 29 Jun. 1970, *G. Davidse & R.W. Pohl 2218* (MO, NY, US); Lago de Yojoa, opposite to Agua Azul, 670 m, 27 Dec. 1977, *R.W. Pohl 13410* (MO).

MEXICO. **Campeche**. Hopelchen, a 20 km al SE de Xpujil, en los terrenos del ejido 20 de Noviembre, 200 m, 18˚26'N, 89˚22'W, 16 Oct. 1996, *P.A.M. Alvarez 621* (MO); Calakmul, loc. a 2 km al W de La Mancolona, canino a La Nueva Vida, 230 m, 18˚48'36"N, 89˚18'50"W, 25 Oct. 1997, *E.M. Martinez S. 29360* (MO); Calakmul, 6 Dec. 1998, *E.M.. Martínez S. & al. 31555* (BM); **Chiapas**. Near the junction of the Río Perlas and Río Jatatè at San Quintin and near Laguna Miramar, 22 Mar. 1955, *E.R. Sohns 1689* (US); 6-12 km S of Palenque on the road to Ocosingo, 12 Oct. 1972, *D.E. Breedlove 28838* (NY); Ocozocoautla de Espinosa, 32 km N of Ocozocoautla on road to Mal Paso, 6 Oct. 1974, *D.E. Breedlove 38201* (NY); Ocosingo, 3 km al S de Frontiera Corozal paralelo al Río Usumacinta, 17 Aug. 1984, *E. Martinéz 7362* (NY); Ocosingo 24 km al SE de Crucero Corozal, camino Palenque-Boca Lacantum, 22 Sep. 1984, *E.M. Martinéz 7725* (NY); Ocosingo, loc. a 9 km al NW de Boca Lacantum, camino a Crucero Corozal-Palenque, 16 Oct. 1984, *E.M. Martinéz S. 8247* (MO); Ocosingo, En Crucero Corozal, camino Palenque-Boca Lacantum, 180 m, 9 Nov. 1985, *E.M. Martinéz S. 15381* (MO); 7 km S of Crucero El Pinal, 2 km NW of El Piedron, at bridge over Río Tilijá, 480 m, 17˚10'N, 91˚45'W, 26 Sep. 1988, *W.D. Stevens & E. Martinez S. 25907* (MO); Ocosingo, 1 km al NW de la Colonia Benito Juárez Miramar, 1 Nov. 1993, *A. Reyes-García 2460* (BM, MO); Ocosingo, 4.1 km al E de Nuevo Guerrero, 299 m, 16°58'56"N, 91°14'47"W, 5 May 2002, *J.C. Soto 23139* (MO); **Oaxaca**. Vicinity of Matias Romero, 7-12 Aug. 1970, *L.H. Harvey 8598* (US); Matias Romero, carretera a Uxpanapa, 17 km al E de Sarabia, 9 km al S de Palomares, 12 Nov. 1978, *S.D. Koch & al. 78244* (MO); Santa Maria Jacatepec, Tuxtepec, camino a Cosolapa San Antonio, 300 m, 17˚51'N, 96˚60'03"W, 20 Feb. 1988, *R. Torres C. 11473* (BM, MO); **Quintana Roo**. Lake Chichancanab (Laguna Chan-kabnab), 28-29 Jul. 1932, *J.R. Swallen 2750* (K, MO, US); Tancah, Quintana Roo, 4-5 Aug. 1932, *J.R. Swallen 2823* (K, US); Brecha camino del Norte, 13 km al E de Leona Vicario, 3 Dec. 1980, *E. Cabrera 440* (MO); **Veracruz**. Campo Experimental Veracruz, de Hule, Ela Palmar, Zongolica, 28-31 Oct. 1943, *J.V. Santos 2650* (NY); Mecayapan, between Volcán Santa Marta and Volcán San Martin Pajapan, 7.5 km NE of Tatahuicapan, on dirt road to Benigno Mendoza, 18°19'N, 94°46'W, 16 Jul. 1982, *M. Nee & al. 25085* (MO, NY); Veracruz, Catemaco 5 km, al este de Pen de Moreno, 3 Oct. 1986, *J.J. Ortiz 1087* (MO).

NICARAGUA. **Jinotega**. Salto Kayaka, Río Bocay, 190-340 m, 13˚51'N, 85˚22'W, 7 Mar. 1980, *W.D. Stevens & al. 16500* (MO); **Matagalpa**. Las Brisas, 15 km al W de Waslala, carretera a El Tuma, 250-300 m, 13˚15'N, 85˚28'W, 23 Dec. 1982, *P.P. Moreno 19230* (MO).

(6) ***Lasiacis harrisii*** Nash, Torreya 13: 274. 1913. (Fig. 18).

Type: *Jamaica, vicinity of Cinchona, Cinchona to Strawberry Hill, 2-10 Sep. 1906, Marble 222* (holotype: NY! [barcode NY00071107]).

Description

Perennials, caespitose. *Culms* 1-5 m long or more, smooth and glabrous, slender, proximally erect arching upward, usually climbing or clambering into the vegetation; *internodes* 2-4(-5) mm thick, glabrous, upward with a line of hairs; *nodes* glabrous; *primary branches* 1 per node, *secondary branches* 2 per node or more usually fascicled. *Leaf sheaths* glabrous, sometimes sparsely pubescent, but always glabrous at maturity, upper margin usually ciliate with hairs 1.0-1.5 mm long, hairs at the auricle prominent; *collars* glabrous; *ligules* 0.5-0.7 mm long, membranous, glabrous; *blades* 5-12(-14.0) cm long, 0.8-1.0 cm wide, linear, acuminate, the base slightly asymmetrical, glabrous, often slightly pubescent at the base with a scabrid margin. *Panicles* small and narrow at base, 2-8 cm long, enfolded in the upper sheath. *Spikelets* 3.5-4.5 mm long, curved less than 45° from the main axis; *lower glumes* 2.0-2,5 mm long, 8 or 9-veined; *upper glumes* 8-9-veined; *sterile florets* without a flower, *paleas* ¾ to subequal to the length of the fertile floret, *lemmas* 8-9-veined; *fertile florets* 3-4 mm long, 1.7-2.0 mm wide elliptic; *anthers* 1.8-2.0 mm long, white, *stigmas* purplish; *caryopses* 2 mm long, 1.5 mm wide. *Chromosome number*: $n = 18$ (Davidse 1972, 1978).

Distribution

Dominican Republic, Jamaica, Puerto Rico, Virgin Islands, Windward Islands. (Fig. 19).

Distribution (bibliographic references)

Nash (1913); Hitchcock and Chase (1917); Hitchcock (1920, 1936); Swallen (1931); Adams (1972); Davidse (1978); Fournet (1978); Cialdella and Vega (1996).

Ecology

Montane cloud forests, usually above 800 m up to 1500-1600 m.

Phenology

October through December.

Remarks

Davidse (1978) expresses some doubts about the clear distinction between *L. harrisii* and *L. divaricata* due to some morphological variation between the two species, particularly in some Caribbean areas (Dominican Republic, Windward Islands). *Lasiacis harrisii* is synonymized within *L. divaricata* by Santos and Sano (2001), Zuloaga et al. (2003), Acevedo-Rodríguez (2005), Giraldo-Cañas (2011), Acevedo-Rodríguez and Strong (2012), Ulloa Ulloa et al. (2025) and in Lindeman and Stoffers (1963: 181) as *L. divaricata* var. *leptopstachya*. In our opinion, the two species mentioned above have distinct characteristics and deserve to be considered distinct mainly for their habitus, the size of the spikelets and their orientation.

Lasiacis harrisii is here considered an endemic species restricted in a small Caribbean area (Fig. 19) with its center of distribution in the highlands of Jamaica showing a similar pattern of distribution as other *Lasiacis* species restricted to the Caribbean hotspots (Smith et al. 2004; Francisco-Ortega et al. 2007) and nearby Neotropical territories such as *L. divaricata*, *L. grisebachii*, *L. rugelii*.

Selected specimens

DOMINICAN REPUBLIC. Cordillera Central, Vega, Jarabacoa, at the falls of Río Jimensa, 18 Nov. 1929, *E.L. Ekman 14176* (K, US).

Figure 18. *Lasiacis harrisii* Nash: **A1**. Habit [A1. from *A.S. Hitchcock 588* (L)]; **A2**. Habit; **B**. Erect spikelet lateral view; **C**. Fertile upper floret dorsal view; **D**. Fertile upper floret ventral view without lower persistent palea; **E**. Fertile upper floret ventral view with lower persistent palea; **F**. Ligular area [A2-F. from *A.S. Hitchcock 9730* (L)]. *A. Maury delineavit*.

Figure 19. *Lasiacis harrisii* Nash: general geographic distribution.

JAMAICA. Jamaica, 26 Dec. 1887, *H.F.A. von Eggers 3121* (NY); Jamaica, *G.S. Jenman 35* (K); **St. Mary**. Below Cold Spring Gap, south side, 3 Nov. 1912, *W. Harris 11354* (BM, NY, US); **Cinchona**. Below Cinchona, north slope of St. Catherine's Peak, 29 Oct. 1912, *A.S. Hitchcock 9730* (L, US); **Portland**. Abbey Green, Blue Mts., 4 Oct. 1912, *A.S. Hitchcock 588* (BM, BR, G, K, L, MO, NY, P, US, W); Blue Mts., Abbey Green, 22 Jan. 1913, *W. Harris 11587* (BM, C, K, MO, NY, P, US); Along road between Section & Hardwar Gap (at "Muriel's Rock), 3400 ft, 30 Mar. 1963, *G.R. Proctor 23405* (BM, IJ); Portland Parish, Muriel's Rock, along road between Section & Hardwar Gap, 24 Nov. 1971, *G. Davidse & G. Proctor 3242* (MO, NY, US), ***n* = 18!** (Davidse 1978); Blue Mountains, Nanny Falls (upper), on dry waterfall, on rocks, 24 Dec. 1973, *B.D. Morley & C. Whitefoord 758* (MO, US); **St. Andrew**. Blue Mts., Mount Faraway, 3 Dec. 1912, *W. Harris 11486* (BM, IJ, K, NY); Blue Mts., Strawberry Hill, 3 Dec. 1912, *W. Harris 11487* (BM, C, K, MO, NY, P, US); Base of Catherine Peak, 3 Jan. 1913, *W. Harris 11552* (BM, C, K, MO, NY, P, US); Chestervale, 9 Jul. 1963, *G.R. Proctor 23834* (BM, IJ); Along track between Guava Ridge and Bellevue, Port Royal Mts., 11 Oct. 1964, *G.R. Proctor 25592* (BM); Hill just above Yallahs River Bridge below Chestervale, 24 Nov. 1971, *G. Davidse & G.R. Proctor 3248* (MO, NY, US); Farm Hill, 22 Oct. 1927, *C.R. Orcutt 3544* (K, MO, US); **St. Thomas**. Farm Hill, 22 Oct. 1927, *C.R. Orcutt 3544* (K, MO, US); Vicinity of Whitfield Hall, climbing grass, common, ca. 4100 ft, 7 Dec. 1954, *G.R. Proctor 9585* (IJ).

PUERTO RICO. Monte Alegrillo, vicinity of Maricao, 20–23 Oct. 1913, *A. Chase 6228* (L, US); Vicinity of Cayey, 3 Dec. 1913, *A. Chase 6742* (US).

VIRGIN ISLANDS. St. John. Coral Bay Quarter, dirt road to Bordeaux Mountain, 9 Jan. 1990, *P. Acevedo-Rodriguez 3169* (NY) .

WINDWARD ISLAND. Dominica. St. John Parish, Cabrit Swamp, 2 Nov. 1964, *D.H. Nicolson 1893* (BM, US); Morne Espanol, 15°31.60'N, 61°27.84'W, 190 m, 16 Aug. 2002, *S. Zona 951* (FTG); **Martinique**. 17 Oct. 1919, *A.S. Hitchcock 16468* (US); Tivoli, 18 Jan. 1943, *s.coll. s.n.* (P); **St. Eustatius**. 1906, *I. Boldingh 750* (C); **St. Lucia.** Forest near Dewey, 1 Nov. 1888, *G.A. Ramage s.n.* (K).

(7) *Lasiacis ligulata* Hitchc. & Chase, Contr. U.S. Natl. Herb. 18: 337. 1917. (Fig. 20).

Type: *Trinidad, above St. Anns, near Port Spain, among bushes along stream, high climbing, 28 November 1912, A.S. Hitchcock 10007* (= Am. Grass Natl. Herb. No. 589) (holotype: US! Two sheets [barcode US00134109, US00134110]; isotypes BM! [barcode BM000938722], BR! [BR0000006863142], DAO (photo!) [barcode DAO000465664], C! [barcode C10017034], F (photo!) [barcode F0046800F]; G! [G00176059], GH (photo!) [barcode GH00023862], K! [barcode K000309328], L! [barcode L0044660], MO! [Acc. No. MO115985], NY! [barcode NY038128], P! [barcode P00633955], PH (photo! [barcode PH00016893], S (photo!) [Acc. No. S05-5477], W! [Acc. No. W19220009713]).

(=) *Panicum glutinosum* Lam., Tabl. Encycl. 1: 174, tab. 43, fig. 3. 1791, non Sw. (1788), *nom. illeg.* - "*Amer. Merid. Insulare Franciae*" (Lamarck 1791: 174).

Type: "*de Cayenne, Stoupy*". (**lectotype, designated here**: P! [barcode 00563917],; isolectotypes P! Two sheets [barcode P00563917, P00563916]; US! Fragment from P [barcode US00148536]).

(≡) *Panicum agglutinans* Kunth, Enum. Pl. 1: 120. 1833, based on *P. glutinosum* Lam. (1791).

(≡) *Panicum divaricatum* L. var. *agglutinans* (Kunth) Hack. ex Sodiro, Anales Univ. Centr. Ecuador 1889: 5. 1889.

(=) *Panicum divaricatum* L. var. *puberulum* Griseb., Fl. Brit. W. Ind. 551. 1864. – Type: *Trinidad, Mr. Crueger s.n.* (holotype: GOET! [barcode GOET001983]).

(-) *Panicum maculatum* Rchb. ex Schlecht. & Cham., Linnaea 6: 33 1831, non Aubl. (1775), *nom. inval.* as *syn.* of *P. latifolium* L. (1753) (missapplied).

(-) *Panicum fruticosum* Salzm. ex Steud., Syn. Pl. Glum. 1: 74. 1854, *nom. inval.,* as *syn.* of *P. latifolium* L. (1753) (missapplied).

Nomina nuda

Panicum megacarpum Steud. in Lechl., Berb. Amer. Austr. 56. 1857, *nom. nud.*
Panicum divaricatum L. var. *puberulum* Sodiro, Anales Univ. Centr. Ecuador: 5. 1889, *nom. nud.*, non Griseb. (1864).

Description

Perennials, robust caespitose. *Culms* 1-5(-10) m tall, erect at the base, arching upward; *branches* solitary or fascicled at the nodes; *internodes* glabrous or with a line of hairs on the side; *nodes* as much as 1-2 cm in diameter, glabrous. *Leaf sheaths* glabrous, pubescent, the overlapping sheath margin ciliate or completely glabrous; *collars* sparsely to totally puberulent, rarely glabrous; *ligules* 2-4(-5.0) mm long, very variable in length, membranous, dark brown, glabrous or pubescent, margin ciliate, hairs 0.5-2.5(-3.0) mm long, apex glabrous or ciliolate; *blades* very variable in length, (5-)8-15(-18) cm long, (0.5-)1.0-3.0(-4.5) cm wide, ovate-lanceolate, acuminate, base asymmetrical, glabrous or puberulent, sometimes ciliate with long hairs, margin scabrid. *Panicles* up to 8 or 9 cm long, ovoid, terminating with numerous branches, longest branch usually reflexed, usually bearing 5-10 short pedicelled spikelets. *Spikelets* 3-4(-5.0) mm long, obovoid, purplish at immaturity, and purplish black at maturity; *pedicels* scabrid; *lower glumes* 1.5-2.5 mm long, 5-11-veined; *upper glumes* 2.5-3.0 mm long, 8-11-veined; *sterile florets* without a flower, *lemmas* 8-11-veined, *paleas* ¾ to equal the length of the fertile floret; *fertile florets* 2.8-4.0 mm long, 2.0-2.5 mm wide, *anthers* 2 mm long, white, *stigmas* white; *caryopses* 1.8-2.0 mm long, 1.5-1.9 mm wide. $2n = 36$ (Gould and Soderstrom 1967); *Chromosome number*: $n = 18$ (Davidse 1972, 1978).

Iconographs

Fig. 135 E (Smith et al. 1982); Fig. 40 E-F (Renvoize 1984); Fig. 53 A-G (Judziewicz 1990); Fig. 153 F-J (Judziewicz 1997); Fig. 87 C (Renvoize 1998); Fig. 96 (Davidse 2004); Fig. 182 H-K (Acevedo-Rodríguez 2005).

Vernacular names

Tobago: "*tibise*" *L.M. Andrews 610A* (NY); **Bolivia**: Santa Cruz, "*tacuarilla*" *R. Guillën & S. Coria 1418* (US); **Brazil**: Acre, "*taquari*" *M. de Pardo & al. 139* (HPZ, MO, NY); Acre, "*taboquinha*" *G.T. Prance & al. 13723* (K, MO, NY, US); Amapá, "*taboca*" *R.S. Cowan & B. Maguire 38105* (NY, US); Bahia, "*taquara*" *J.G. Jardim & al. 1115* (MO), "*taquari*" *E.B. dos Santos & A.S. Barreto 69* (CEPEC, K), *T.R. Soderstrom & al. 2190* (CEPEC, US); Mato Grosso: "*rabo de raposa*" *J.A. Ratter & al. 1998* (K, NY, P, US); Minas Gerais: "*taquari*" *Y. Mexia 5328* (BM, G, K, MO, NY, P, US); Pará, "*gavinho*" *A. Goeldi 227* (US, W); "*taboca*" *E. Fittkau & D. Coelho 118* (NY), "*taboquinha, taquari*" (Smith et al. 1982); Pernambuco, "*taquara-de-apito*" *A. Ferreira 125* (K, MO, US); Santa Catarina, "*taquari*" (Smith et

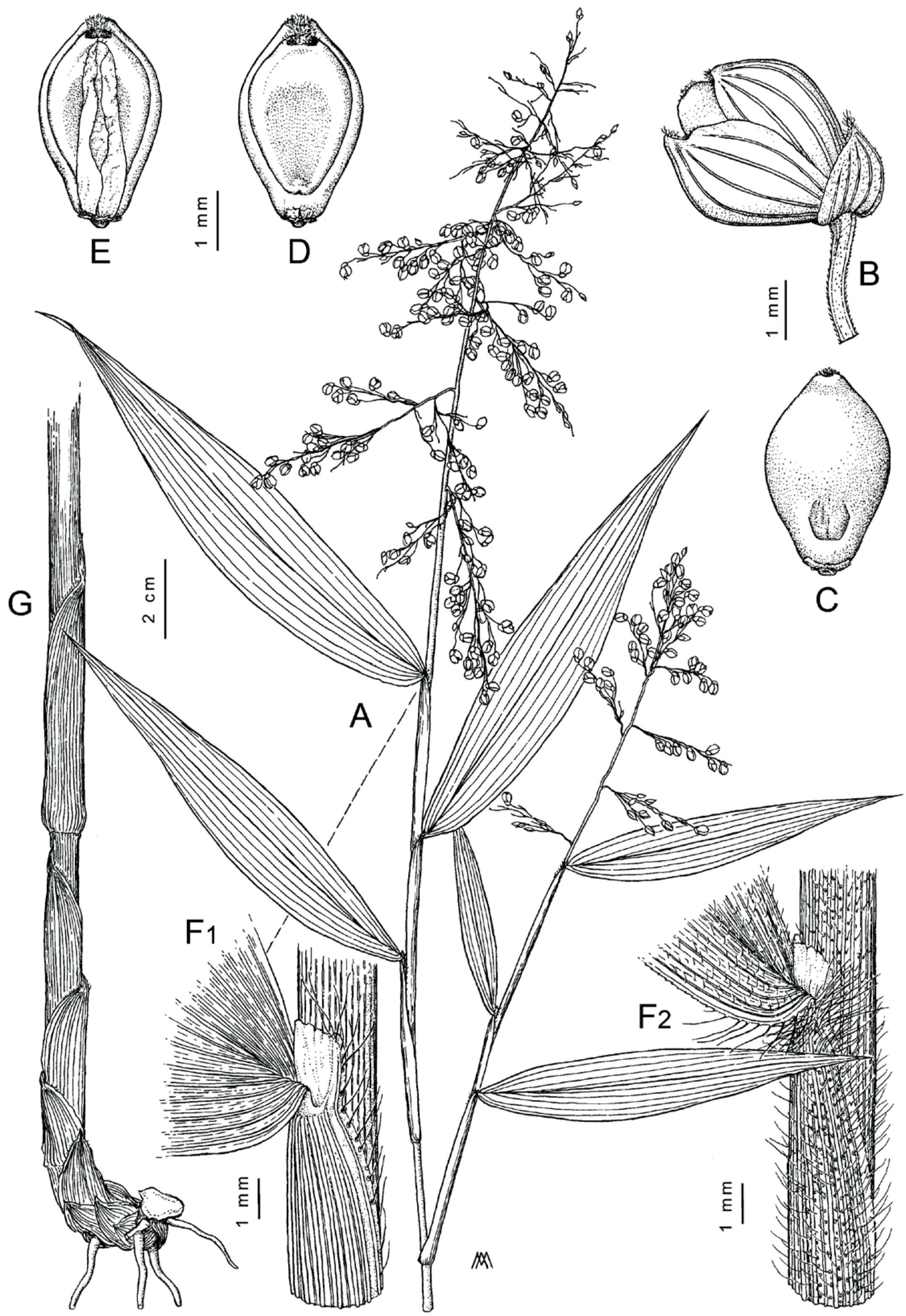

Figure 20. *Lasiacis ligulata* Hitchc. & Chase: **A**. Habit; **B**. Spikelet lateral view; **C**. Fertile upper floret dorsal view; **D**. Fertile upper floret ventral view without lower persistent palea; **E**. Fertile upper floret ventral view with lower persistent palea; **F1**. Ligular area, leaf sheath glabrous; [A-F1. from *M.J. Jansen-Jacobs & al. 6099* (K)]; **F2**. Ligular area, leaf sheath pilose; **G**. View of the culm with persistent leaf sheath. [F2-G. from *R.R. de Santos, & al. 1264* (K)]. *A. Maury delineavit.*

al. 1982); **French Guiana**: "*calumet*", "*pen:pē*", "*tawkalipiñú*" (Judziewicz 1990); **Perú**: Jaen, "*bombilla*", "*bombilla de muerta*" *F.R. Fosberg 27757* (MO, US); San Martín, "*carrizo*" *R. Ferreira 7916* (US); Uyacali, "*carricillo*" *J. Graham & J. Schunke Vigo 516* (F); "*náng-kuchip*" (Quattrocchi 2006); **Suriname**: "*bamboesigras*", "*kapoeweri bamboesi*" (Amshoff and Henrard 1948; Judziewicz 1990), "*bambusigrasi*" (van't Klooster et al. 2003).

Ethnobotanical and economic uses

Bolivia: Beni, "*fruit used in dental use as blister mouth*" (Zambrana et al. 2017); **Ecuador**: "*culm used to make Shuar instrument* "*kantash*" (Bennet 1990).

Distribution

Bolivia, Brazil, Colombia, Dominican Republic, Ecuador, French Guiana, Guyana, Leeward Islands, Paraguay, Perú, Puerto Rico, Suriname, Trinidad & Tobago, Venezuela, Virgin Islands, Windward Islands (Fig. 21). The presence of *L. ligulata* in Mexico is erroneously reported in Santos and Sanos (2001).

Distribution (bibliographic references)

Hitchcock and Chase (1917); Hitchcock (1915, 1920, 1927a, 1936); Nash (1931); Amstoff and Henrard (1948); Lemée (1955); Pinto-Escobar (1966); Smith et al. (1982); Killeen (1990); Howard (1979); Davidse (1978, 2004, 2008); Cialdella and Vega (1996); Foster (1966); Judziewicz (1990, 1997); Renvoize (1984, 1998); Santos and Sano (2001); Zuloaga et al. (2003); Hollowell et al. (2004); Acevedo-Rodríguez (2005); Renvoize et al. (2006); Davidse et al. (2007); Reeves et al. (2007); Hokche et al. (2008); Morrone et al. (2008); Giraldo-Cañas (2011); Acevedo-Rodríguez and Strong (2012); Dorr (2014); Villavicencio et al. (2014).

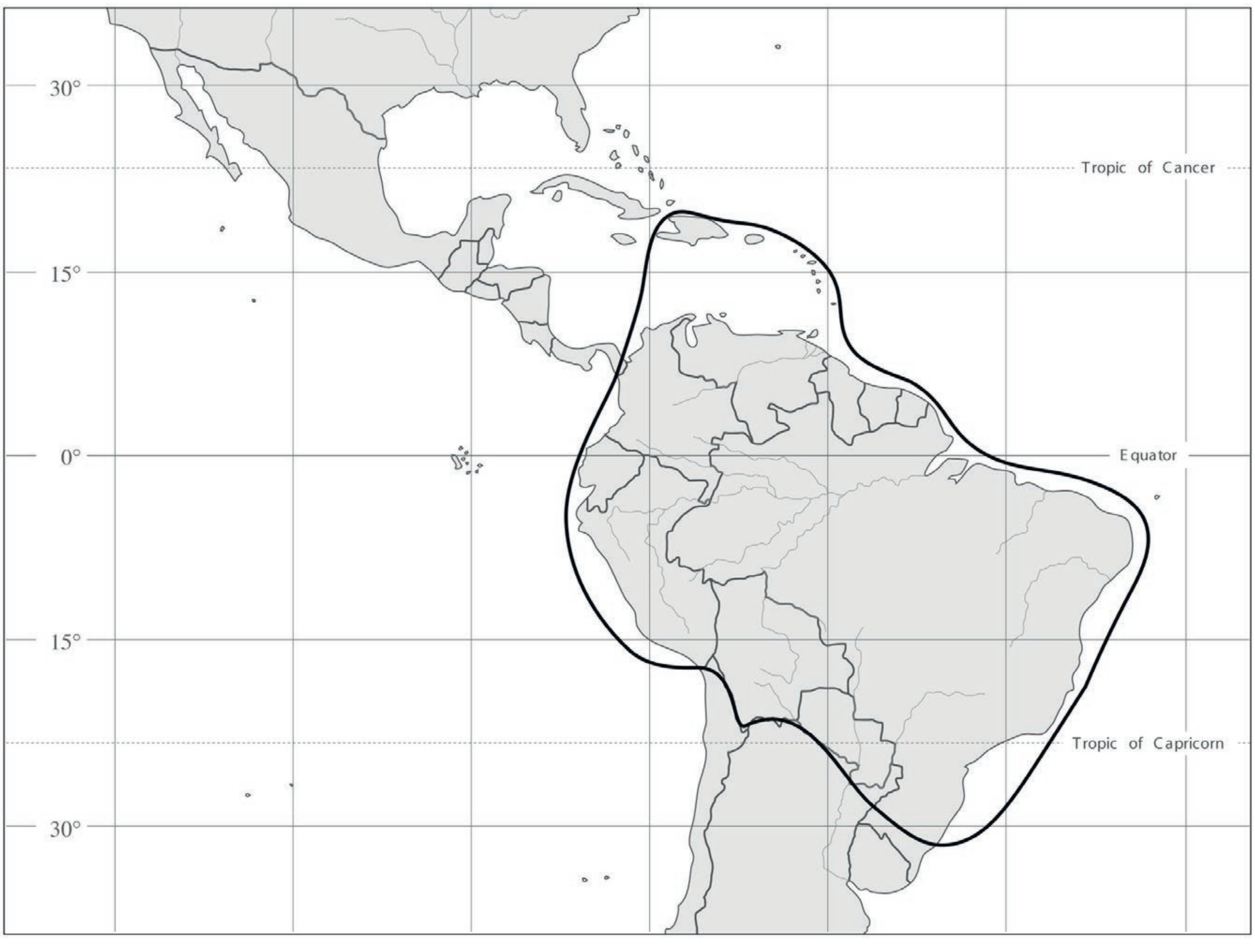

Figure 21. *Lasiacis ligulata* Hitchc. & Chase: general geographic distribution.

Ecology

Primary and secondary forests, riverbanks, roadsides, and forest clearings. Mostly below 1000 m, except in northern South America where it can reach up to 2400 m (Perú: Amazonas, *J.J. Wurdack 1048* (K, NY, US).

Phenology

Caribbean, and Central America June through March; southern South America, March through September.

Remarks

The specimens in P-Lamarck under several names: "*P. arborescens*", "*P. viscosum*", "*P. glutinosum*" were correctly identified by G. Davidse as *L. ligulata* in 1974 in contrast with A. Lourteig's misinterpretation as *L. maculata* in 1983. At US there is a fragment taken from a Lamarck's specimen [barcode US00148536] by A.S. Hitchcock, who made a sketch from the Lamarck's specimen.

According to the comments above, the previous typification of *Panicum glutinosum* Lam. (Baldini 2010: 114) must be rejected due to a misinterpretation of the Tab. 43, fig. 3 in Lamarck (1791). A direct examination of Lamarck's original material at P turned out decisive to correctly interpret the Lamarckian name above and shows how misleading images alone may sometimes be in typification issues.

Lasiacis ligulata is distributed mainly in the Caribbean area, particularly the West Indies, and northern South America, e.g. in the Guianas and northern and northeastern Brazil. The ligule, up to 5 mm long, is not the only character that appears at first sight and the reclined orientation of the inflorescences is another immediate diagnostic character, with the density of the spikelets greater than in *L. divaricata* var. *divaricata*. The pubescence is very variable and does not show a specific geographical signal as in *L. maculata*. Glabrous forms can be found in Brazil, except for the hairs on the collar, and again in Peru and Bolivia as dominant form. Alves da Silva et al. (2001) found the presence of arbuscular mycorrhizae in *L. ligulata*.

Selected specimens

BOLIVIA. Beni. Ballivián, San Borja, 58 km hacia La Paz, 270 m, 19 Jul. 1981, *S. Beck & al. 6874* (K, US); Prov. Vaca Diez, Riberalta, alrededor de la Estación Experimental de IBTA, 170 m, 11°00'S, 66°04'W, 22 May 1987, *J.C. Solomon 16698* (MO); Vaca Diez, Alto-Ivón, Aug. 1992, *S. Bergeron 315* (K); **Cochabamba**. Cochabamba, Jun. 1909, *O. Buchtien 2499* (US); Carrasco, km 240 en la carretera Santa Cruz-Villa Tunari, 290 m, 64°46'W, 17°00'S, 8-9 Jul. 1989, *H.H. Smith & al. 13637* (K, MO, NY); **La Paz**. Iturralde, Siete Cielos, Río Manupare, 180 m, 12°27'S, 67°37'W, 10 Jun. 1987, *J.C. Solomon 17024* (K, MO); Sud Yungas, Alto Beni, 23 Jul. 1987, *R. Seidel 2089* (K); Nor Yungas, Alto Beni, carretera del puente Sapecho a Boopi, 450 m, 26 May 1988, *R. Seidel 2463* (K, MO, US); Prov. Iturralde, Basin of Río Beni/Río Turchi, 320 m, 14°35'S, 67°35'W, 10 May 1990, *D.C. Daly 6386* (MO, NY); Abel Iturralde, Parque Nacional y Area de Manejo Integrado Madidi, 450 m, 14°24'S, 67°57'W, 22 Apr. 1997, *N. Paniagua Z. 1130* (K, MO); Franz Tamayo, Parque Nacional y Area Natural de Manejo Integrado Madidi, NW de Apolo, Asariamas, Río Resina, 700 m, 14°19'48"S, 68°33'35"W, 20 May 2005, *L. Cayola 1678* (MO); **Madre de Dios**. Near the confluente of Río Tambopata and Río La Torre, 39 km of Puerto Moldonado, 7 Jul. 1987, *S.F. Smith & al. 909* (G); **Pando**. Along Río Madre de Dios, Sena, 125 m, 11°28'S, 67°14'W, 4 Sep. 1985, *M. Nee 31755* (K, MO, NY); Abuná, Nacebe el Río Orthón, 11 Oct. 1989, *S. Beck & al. 19303* (K); Abuná, Río Orthón, 8 Jul. 1992, *H. Vargas & P.F. Foster 746* (K); **Santa Cruz**. Santiago de Chiquitos, 680 m, 2 Sep. 1942, *H. Carter 7007* (US); Nuflo de Chávez, Ascención de Guarayos, 30 Aug. 1985, *S. Beck 12287* (US); Velasco, 200-250 m, 13°35'S, 60°56'W, 25 Jun. 1991, *M. Nee 41359* (K, MO); Ichilo, old meander loop of Río Ichilo, 1-1.5 km SW of Highway from Buena Vista to Villa Tunari, 245 m, 17°18'S, 64°12'W, 17 Jul. 1994, *M. Nee & R. Moran 45215* (MO); Velasco, Reserva Ecologica El Refugio, 15 May 1995, *R. Guillën & S. Coria 3675* (MA); Velasco, Reserva Ecologica El Refugio, 14° 45' 44"S, 61° 02' 53"W, 20 May 1994, *R. Guillën & S. Coria 1418* (US); Between Buena Vista and Amboro Nat. Park, 9 Jul. 1995, *S. Lægaard 17656* (K); 4 km N of Parque Nacional Noel Kempff mercato, Campamento Huanchaca I., 1 Nov. 1995, *P.F. Foster & al. 571* (G), 3 Nov. 1995, *P.F. Foster & al. 595* (G); Parque Nacional Noel Kempff Mercato, 700 m, 14°33'73"S, 60°45'89"W, 20 Jul. 1996, *L. Arroyo & E. Guzmàan 1323* (G, MO); Velasco, Parcela Monte Verde, 288 m, 15°00'37"S, 61°07'42"W, 21 Aug. 1996, *R. Guillén & al. 4585* (G, MO); Ichilo, along trail from Río Yapacaní into Campamento Matacarú of Parque Nacional Amboró, 350 m, 17°32'S, 63°52'W, 31 May 1998, *M. Nee & L. Bohs 49530* (MO); Guarayos, Conscecion maderera La Chonta, 20-30 Jun. 2001, *J.C. Catari & al. 58* (MO); Ichilo, bridge over Río Vibra, 7.5 km ENE of Puerto Grether, 235 m, 17°10'S, 64°16'W, 24 Jul. 2004, *M. Nee 52814* (MO, NY, US); Florida, Bella Vista, 16°29'N, 63°40'W, 3 Feb. 2007, *M. Vargas 342* (NY).

BRAZIL. Brasiliae, s.d., *W.J. Burchell 703* (FI-Webb, L, US), *879 A* (FI-Webb); Brasilia, *L. Riedel s.n.* (FI, G, NY, P, UPS, US), *218* (L), *963* (K, P, US, W), Brasil, s.d., *Martius 675* (FI-Webb, L, MO); Brésil, 1840, *P. Claussen 192* (G); **Acre**. Rio Branco, Surumu, Aug. 1909, *E. Ule 8017* (K); Vicinity of Campinas, 17 Jul. 1968, *E. Forero & al. 6310* (MO, US); Igarapé São Francisco, lower Rio Moa, 9 May 1971, *W.C. Steward & al. P12839* (K, NY, US); Aldeota between Porangaba & Papagaio, Rio Juruá-Mirim, 18 May 1971, *P.J.M. Maas & al. P13109* (K, MO, NY, US, P); Rio Purus, Lago Prêto 2 km N of Lábrea, 26 Jun. 1971, *G.T. Prance & al. 13723* (K, MO, NY, US); Outside of Cruzeiro do Sul, 9 Mar. 1976, *C.E. Calderon & T.R. Soderstrom 2327* (US); Rio Branco, Zoobotanical Garden of Federal University of Acre, 26 Sep. 1980, *S.R. Lowrie & al. 185* (MO, NY); Along road between Cruziero do Sul and Rio Branco, 28 km E of Cruzerio do Sul at Lagoinha, 7°38'S, 72°35'W, 160 m, 24 Aug. 1986, *T.B. Croat 62602* (MO, HPZ); Rio Branco, Parque Zoobotanico, 09°58'S, 67°48'W, 5 Jun. 1991, *D.C. Daly 6856* (HPZ, MO, NY); Rio Branco, Parque Zoobotanico, terra firme, 9°48'S, 67°42'W, 25 May 1995, *C.S. Figueredo & I. Riviero 788* (HPZ, MO); Sena Madureira, Riozinho do Andirà, colocaçao Curitiba, 9°43'747"S, 68°08'854"W, 30 May 1995, *R.S. Oliveira & al. 445* (HPZ, MO); Bujari, Riozinho do Andirà, Fazenda Ipanema, BR 363, 9°44'10"S, 68°08'38"W, 15 Jul. 1995, *M. de Par-*

do & al. 139 (HPZ, MO, NY); Marechal Thaumaturgo, Reserva Extrativista do Alto Juriá, margem direita do Rio Tejo, 3 May 2001, *L.G. Lohmann & E.C. de Oliveira 465* (MO); Senador Guiomard, Catuaba, Fazenda Continenta, 10°04'20"S, 67°37'25"W, 5 Jul. 2001, *K.N. Yoshida Arns & al. 971* (HPZ); **Alagoas:** Munic. de Marechal Deodoro, Alagoas, Ladeira Sumauma, Rio Sumauma, 17 Oct. 1986, *A.C. Sarmento & al. 888* (CEPEC); Murici, EE de Murici, borda da mata, 9°16'16"S, 35°54'17"W, 14 Nov. 2002, *M.J.N. Rodal 1325* (CEPEC, NY); **Amapá**. Serra do Navio, Rio Amapari, 1 Nov. 1954, *R.S. Cowan & B. Maguire 38105* (NY, US); Santa Catarina, Morro da Fazenda, Itajaí, 100 m, 22 Apr. 1955, *R. M. Klein 1320* (US); Rio Oiapoque, Boa Esperança, 3°12'N, 52°19'W, 18 Aug. 1960, *W.A. Egler 47665* (K, NY, US); Rio Oiapoque, 15 Oct. 1960, *J.M. Pires 48844* (K, US); Rio Araguari, near Porto Platón, 0°44'N, 51°22'W, 17 Sep. 1961, *J.M. Pires & al. 51007* (K, NY, US); Vicinity of Igarape Ariramba, 1°13'N, 51°3'W, 4 Aug. 1962, *J.M. Pires & P.B. Cavalcante 52353* (MO, NY, US); **Amazonas**. Nov. 1849, *R. Spruce 412* (K, NY); Autaz-Mirim, Rosa Branca, 14 Jun. 1973, *A. Loureiro & al. 38879* (NY); Behind São Paulo de Olivença, 16 Aug. 1973, *E. Lleras & al. P17333* (K, NY, US); 2 km S of Maués, E shore of Maués River, surrounding Guaraná farm, 27 Apr. 1974, *D.G. Campbell 22147* (K, NY, US); Transamazon Highway, 7.2 km above Igarapé Mafuí, ca. 159 km E of Humaitá, 14 Jun. 1979, *C. Calderón & al. 2522* (K, MO); Bank of Rio Abacaxis, accross from Axinim, 58°41'W, 4°10'S, 8 Jul. 1983, *S.R. Hill 13012* (K, MO, NY); SWW of Manaus, road from Cacau Pirera to Manacapuru, 6 Aug. 1987, *S. Tsugaru & Y. Sano B-729* (NY); **Bahia**. In sylvis prope Bahia, *M. Salzmann s.n.* (FI, P); Vicinity of Bahia, 3 Dec. 1924, *A. Chase 8027* (US); Margem da Rodovia Itabuna-Ilhéus, mata úmida, 30 Aug. 1965, *R.P. Belém 1657* (CEPEC, US); Potiragua, ca. 48 km N of Itapebí, 5 Apr. 1976, *T.R. Soderstrom & al. 2132* (CEPEC, US); Porto Seguro, Reserva Biologica do Pau Brasil (CEPLAC), 35 m, 7 May 1976, *T.R. Soderstrom & al. 2190* (CEPEC, MO); Sta. Cruz de Cabrália, Torre da Embratel, rodoviaria Eunápolis/Porto Seguo, 17 Aug. 1978, *S. Mori & al. 10767* (CEPEC, K); Itamarajú, ca. 5 km ao NW de Itamarajú, 3 Jul. 1979, *L.A. Mattos Silva & al. 537* (CEPEC); Salvador, 11°09'S, 40°00'W, 15 Aug. 1979, *R. Souza & S. Sant'Ana 10115* (CEPEC); Cachoeira-Vale dos Rios Paraguaçu e Jacupé, Aug.-Sep. 1980, *Costa 641* (CEPEC, HUEFS, K); Chapadão Ocidental da Bahia, by Correntina, 13°20'S, 44°38'W, 26 Apr. 1980, *R.M. Harley & al. 21784* (K, MO, P); Estação Ecológica Pau-Brasil, 22 Apr. 1982, *A.M. de Carvalho & al. 1314* (K); Jacobina, Serra do Brite, 23 Aug. 1980, *W.N. da Fonseca 323* (CEPEC, US); Ilhéus, km 2 a 3 do ramal de baixo para o Povoado de Sambaituba, 10 m, 8 Aug. 1980, *L.A. Mattos Silva & J. L. Hage 1007* (CEPEC, K, US); Ilhéus, Fazenda Barra do Manguinho, 29 Sep. 1980, *L.A. Mattos Silva & al. 1101* (CEPEC); Municipio de Santa Cruz de Cabralia, 16 Jul. 1981, *H.S. Brito & S.G. da Vinha 03* (G); Ilhéus, area do CEPEC, 29 Jul. 1981, *J.L. Hage & H.S. Brito 1134* (CEPEC, K); Sta. Cruz Cabrália, cerca 16 km W de Porto Seguro, 29 Aug. 1983, *T.S. dos Santos 51* (CEPEC, G); Ilhéus, CEPEC, 8 Sep. 1983, *E.B. dos Santos & A.S. Barreto 69* (CEPEC, K); Santa Cruz Cabrália, cerca 16 km a W de Porto Seguro, 8 Aug. 1984, *R. Souza & al. 427* (CEPEC); Lamarão do Passé, 12°31'S, 38°24'W, 21 Nov. 1984, *L.R. Noblick 3384* (CEPEC, HUEFS); Lamarão do Passé, 21 Nov. 1984, *L.R. Noblick 4109* (K); Ilhéus, CEPEC, 24 Jul. 1986, *J.L. Hage 2109* (CEPEC, G); Feira da Santana, BA-052, 25 km NW do entrocamento c/BR-116, 12°10'00"S, 39°11'17"W, 22 Nov. 1986, *L.P. De Queiroz 1383* (HUEFS); Ilhéus, grounds of CEPEC, 24 Nov. 1987, *P.J.M. Maas & al. 6966* (CEPEC); Belmonte, districto de Barrolandia, EGREB, Rodovia Itapebí/Belmonte, mata igrofita bahiana, 30 Mar. 1988, *R. Souza 840* (CEPEC); Jussari, ca. 7 km na estrada de Jussari para Palmira, 21 Sep. 1990, *A.M. de Carvalho & W. Thomas 3196* (CEPEC, HUEFS, K); Uruçuca, Serra Grande, 14°25'S, 39°01'W, 11-21 Sep. 1991, *A.M. de Carvalho & al. 3532* (CEPEC, HUEFS, K, NY, US); Near Teixera de Freitas, Rod. BR-101, 13 Apr. 1992, *G. Hatschbach 57047*; Belmonte, Barrolandia, Est. Experimental "Gregorio Bondar" CEPLAC, 48 km E of BR 101 on road to Belmonte, 16°08'S, 39°15'W, 13 May 1993, *W. Thomas & al. 9927* (K, MO, US); Prado, 10 km N of Prado on coast road to Cumuruxatiba, 17°17'S, 39°18'W, 19 Oct. 1993, *W. Thomas & al. 9982* (CEPEC, NY); Prado, on road from Itamaraju to Cumuruxatiba, 10.5 km NE of turn off road to Prado on road to Cumuruxatiba, 1708'S, 3925'W, 20 Oct. 1993, *W.W. Thomas & al. 10027* (MO); Una-Bahia, 20 Jul. 1994, *J.G. Jardim & al. 503* (CEPEC, NY); Ilhéus, àrea do CEPEC, mata higrofila Sul Baiana, coletas efetuadas em área de cacau abandonado, 6 Aug. 1996, *J.G. Jardim & al. 871* (CEPEC, G, NY); Municipio de Una, Reserva Ecologica do Mico-leão (IBAMA), entrada del km 46 de la Rodovia BA-001 Ilhéus-Una. Región de la Mata Higrófila Sud Bahiana, camino que leva a la Faz Jaqueival, interior de mata, 15°09'S, 39°05'W, 14 Aug. 1996, *M.S. Ferrucci, & al. 1053* (MA); Ilhéus, Campus da Universidade Estadual de Santa Cruz, 4 Sep. 1996, *L.A. Mattos Silva 3489* (CEPEC); Almadina, on road to Ibatupà, 14°44'11"S, 39°41'57"W, 4 Apr. 1997, *W.W. Thomas & al. 11431* (NY); Porto Seguro, Prque Nacional Monte Pascola, 16°52'02"S, 39°24'54"W, 17 Jul. 1997, *W.W. Thomas & al. 11570* (NY); Almadina-Bahia, Rod. Almadina/Ibitupã, 12 Sep. 1997, *J.G. Jardim & al. 1115* (HUEFS, NY); Jussari, Rodovia Jussari/Palmira, 39°31'43"W, 15°09'29"S, 7-8. Nov. 1998, *A.M. Amorin & al. 2607* (CEPEC, NY); Salvador de Bahia, Região Metropolitana, 12°58'S, 38°30'W, 13 Nov. 1998, *M.L. Guedes 6654* (CEPEC, HUEFS); São Gonçalo dos Campos, 15 Nov. 1998, *M. Vanilda 130* (HUEFS); Santa Teresina, Serra da Jibóia, ca. 4 km de Pedra Branca, 12°51'10"S, 39°28'32"W, 27 Sep. 2000, *L.P. De Queiroz 6379* (HUEFS); Uruçuca, área da EMARC, Reserva Gregório Bondar, mata igrofita Sul Baiana, 14°36'8"S, 39°16'27"W, 23 Sep. 2000, *S. Sant'Ana 996* (CEPEC, NY); Jussari, Serra do Teimoso, 1 Sep. 2001, *R.P. Oliveira 737* (HUEFS); Margem da estrada Barra da Estiva-Mucugê, 13°7'3''S, 41°29'13''W, 1105 m, 28 Feb. 2002, *A.M. Giulietti & R.M. Harley 2064* (HUEFS); Floresta Azul, entrada a ca. 12 km à esq. estrada de Floresta Azul para Itapetinga, Haras Binau, no interior da mata atlantica, 23 Apr. 2003, *P. Fiaschi 1512* (CEPEC); Esplanada, Linha Verde, 12°2'13"S, 37°42'17"S, 17 Aug. 2003, *K.R.B. Leite 315* (HUEFS); Almandina, ca. 4 km da estrada Almandina-Coaraci, enrada à esq. Fazenda São José, 14°43'S, 39°36'W, 2 Oct. 2003, *P. Fiaschi 1629* (CEPEC, MO, NY); Barro Preto, Serra da Pedra Lascada, 13,7 km de Barro Preto, 600-900 m, 14°46'13"S, 39°12'10"W, 29 Sep. 2004, *A.M. Amorin 4220* (HUEFS, MO); Senior e Bonfim, Serra de Santana, 10°21'55"S, 40°11'55"W, 28 Jul. 2005, *T.S. Nunes 1213, 1222* (HUEFS); Bahia, Arataca, Serra do Peito-de-Moça, completo Serra das Lontras, 15°10'25''S, 39°20'30''W, 12 Oct. 2005, *A.M. Amorin 5278* (HUEFS); São Desiderio, 12°31'2"S, 45°5'46"W, 17 Jun. 2007, *G. Araújo 147* (HUEFS); Santa Terezinha, Serra da Jibóia, Serra da Pioniera, 12°45'S, 39°32'W, 4 Aug. 2007, *R.P. Oliveira 1373* (HUEFS); Igrapiúna, estrada para Ituberá, Reserva Ecológica da Michelin, mata litoranea, 13°49'S, 39°7'W, 17 Aug. 2007, *R.P. Oliveira 1381* (HUEFS). **Ceará**. Guaramaranga, 23 Jun. 1929, *G. Bolland 38* (K); **Districto Federal**. Praia de Sernambetida (Receio dos Bandeirantes), 23°00'S, 43°20'W, sea level, 4 Apr. 1952, *L.B. Smith 6335* (US); Fazenda Vargem Bonita, ca. 10 km S of Brasilia, 4 Feb. 1966, *H.S. Irwin & al. 12268* (MO, NY, P); Côrrego Landim, ca. 25 km N of Brasilia, 950 m, 15 Mar. 1966, *H.S. Irwin & al.*

13958 (MO, NY, P, US); Parque Municipal do Gama, 1000 m, 21 Mar. 1966, *H.S. Irwin & al. 14155* (C, MO, NY, P, US); **Espírito Santo**. Near Muqui, Morro Bom Retiro, 250 m, 22°57'S, 41°21'W, 23 Apr. 1972, *T.R. Soderstrom & D. Sucre 1957* (CEPEC, K, MO, US); Vitoria, Vila Velha, Morro do Convento de N.Sra. da Penha, 3 May 1974, *D. Sucre 10743* (MO); San Mateus, 7 Aug. 1983, *G. Hatschbach 46792* (CEPEC); Santa Teresa, Valsugana Velha, 6 Mar. 1990, *W. Boone 1357* (HUEFS); Linhares, Reserva Florestal da Campana Vale do Rio Doce, 19°84'S, 40°88'W, 24 Apr. 1990, *L.P. De Queiroz 2473* (HUEFS); Santa Teresa, Aparecidinha, terreno de Luiz Briguenti, 13 Apr. 2003, *R.P. Oliveira 867* (CEPEC, HUEFS); **Goiás**. Rio Araguaya nella foresta Travessão de S. Vicente, 19 Jul. 1899, *L. Buscalioni 4570* (RO); Between Viannapolis and Ponta Funda, 17 Mar. 1930, *A. Chase 11321* (NY); Geral do Paraná, 15 km by road S of São João da Aliança, 1120 m, 21 Mar. 1973, *W.R. Anderson 7537* (K, MO, NY, US); 31 km N of the intersection of Highways BR-153 and GO-54, 650 m, 10 Apr. 1976, *G. Davidse & al. 12241* (MO); Crominia-Mairipotaba, 750 m, 17°20'S, 49°23'W, 27 Apr. 1988, *R.D. Reeves & J.M. Baker 209* (K, MO, NY); Niquelandia, Cidade de Macedo, 20 km N de Niquelandia, 19 May 1993, *T. Filgueiras 2445* (MO); São Domingo, 14 May 2000, *G. Hatschbach & al. 974* (K); **Mato Grosso**. Santa Anna da Chapada, 16 May 1903, *G. Malme 3357* (US); Mato Grosso, S. Anna da Chapada, 1903, *Robert 332b* (K); Vicinity of Dourados, 22°S 54°40'W, 18–21 Feb. 1930, *A. Chase 10969* (NY, US); On the Xavantina-São Felix road, 12°54'S, 51°52'W, 27 Jun. 1968, *J.A. Ratter & al. 1998* (K, NY, P, US); Ca. 300 km N of Xavantina, 12°54'S, 51°52'W, 3 May 1968, *R.R. de Santos, & al. 1264* (K, NY, P, US); Fazenda Suiá Missú, 27 Jul. 1968, *P.W. Richards 6531* (P, US); Cuiabá dos Guimarães, Veu da Novia falls along Rio Coxipozinho at base of falls, 15°24'S, 55°50'W, 21 Oct. 1985, *W. Thomas & al. 4490* (K, MO, NY, US); Chapadão do Sul, 19°01'14"S, 53°00'08"W, 23 Jan. 2001, *M. Groppo & al. 481* (G, K); **Maranhão**. Perizes, 6 Jul. 1954, *G.A. Black & al. 54-16532* (P); Santa Catarina, Itajaì, Morro da Ressacada, 29 Mar. 1956, *P.R. Reitz & R. M. Klein 2951* (G); Lorêto, Ilha de Balsas, between the Rios Balsas and Parnaíba, 7°23'S, 45°4'W, 17 Apr. 1962, *G. Eiten & L.T. Eiten 4320* (K, NY, US); Rio Alto Turiaçu, Nova Esperança, 2°55'N, 45°45'W, 30 Nov. 1978, *J. Jangoux & R.P. Bahia 93* (NY); Codò to Peritorò, 4°34'S, 44°0'W, 28 Sep. 1980, *D.C. Daly & al. D348* (MO, NY, US); Fazenda Bacaba, Doctor Haroldo, 3 km NW of Lago do Junco, 4°26'S, 44°58'W, 4 Oct. 1980, *D.C. Daly & al. D478* (MO, NY, US); Posto Indigena Pindaré, Bom Jardim along Rio Pindaré, ca. 15 km W of Santa Ines, 3°30'S, 45°30'W, 31 Aug. 1983, *M.J. Balick & al. 1491* (MO); Caru Reserve, 9 Jul. 1996, *L. Cormier 88* (MO); **Minas Gerais**. 18 Feb. 1847, *A.F. Regnell 308* (UPS); Serra do Cipó, 110 km NE of Belo Horizonte, 28 Mar.–1 Apr. 1925, *A. Chase 9103* (MO, NY, W); Juiz de Fora, 700 m, 23 Feb. 1925, *A. Chase 8610* (US); Viçosa, road to São Miguel, 20 Nov. 1930, *Y. Mexia 5328* (BM, G, K, MO, NY, P, US); Viçosa, 5 Apr. 1935, *J.G. Kuhlmann 152952* (MO, US); Serra do Espinhaço, NE of Francisco Sá, 12 Feb. 1969, *H.S. Irwin & al. 23138* (BM, MO, NY, US); Chapada dos Veadeiros, ca. 10 km S of Cavalcante, 1000 m, 10 Mar. 1969, *H.S. Irwin & al. 24237* (MO, US); Serra do Espinhaço, 15 km N of São João da Chapada, 23 Mar. 1970, *H.S. Irwin & al. 28160* (MO, NY, P); Marliéria, Parque Estadual di Rio Doce, 450 m, 19°42'S, 42°30'W, 25 Sep. 1975, *E.P. Heringer & G. Eiten 15220* (MO, US); Municipio Trofilo Otoni, along the BR-116, 29 Mar. 1976, *G. Davidse & al. 11500* (K, MO), **n = 18!** (Davidse 1978); Minas Gerais, São João Del Rey, ca. 8 km de Tiradentes em direção à Villa Santa Cruz, 21°07'45"S, 44°12'71"W, 16 Jan. 1994, *A.M. Giulietti & al. 13724* (K); **Pará**. In vicinibus Santarem, Apr. 1850, *R. Spruce (23)* (BM, FI-Webb, G, NY, US, P); Santarem, Apr. 1850, *R. Spruce 795* (K, NY, W); Pará, ad ripas fluminis Amazonum, inter Santarem et Barra do Rio Negro, Oct. 1850, *R. Spruce (17)* (FI-Webb, G, NY, US, W); Pará, Rio Tocantins, nella foresta Igarapé Curiman presso Cametá, 2 May 1899, *L. Buscalioni 1252* (NY, RO); Rio Tocantins, Ilha da Bandeira, 31 May 1899, *L. Buscalioni 2871* (RO); Rio Tocantins, Floresta da Villagem do Lago Vermelho, 23 Jun. 1899, *L. Buscalioni 2959* (RO); Pará, 29 Jun. 1908, *C.F. Baker 392* (G); Pará, Bragança Railroad, Apr. 1914, *A. Goeldi 38* (MO, US, W); Paraná, Yacarchy, 17 Apr 1915, *P. Dusén 14050* (K); Marajó Island, Jun. 1918, *A. Goeldi 227* (US, W); Rio de Janeiro, Niteroi, San Francisco, 23 Sep. 1921, *E.W.D. & M.M. Holway 1148* (US); Santarem, 14 Apr. 1924, *J.G. Kuhlmann 2002* (BM, MO, US); Pará, Santa Isabel, 1–2 Jul. 1934, *J.R. Swallen 5051* (US); Campo east of Fazenda Urucurituba on Rio Tapajos, opposite Fordlandia, 17 Apr. 1943, *W.A. Archer 8403* (US); Belém, on lands of Istituto Agronomico do Norte, 28 Apr. 1944, *A. Silva 168* (K, P, US); Rio Mojú, Fábrica, mata de Najateua, 1 Jun. 1954, *G.A. Black 54-16333* (P); Tiriós, Rio Parù do Oeste, 22 Mar. 1962, *E. Fittkau & D. Coelho 118* (NY); Vicinity of Paragomins, Belém-Brasília, 13 Aug. 1964, *G.T. Prance & N.T. Silva 58699* (K, MO, NY, US, W); Road BR 22, Capanema to Maranhão, vicinity of Cachoeira, 30 Oct. 1965, *G.T. Prance & T.D. Pennington 1823* (K, NY, US); Belém, 13 Dec. 1966, *T.R. Soderstrom 1198* (US); Santarém, km 35 da estrada do Palhão, Ramal para o Novo Imperio, 13 Aug. 1969, *B.M. Silva & R. Souza 2247* (K, MO, NY, US); Cujaba-Santarem, km 890, 14 Feb. 1977, *J.H. Kirkbride & E. Lleras 2764* (US); Km 858, Rio Escorpiao, Serra do Cachimbo, 430 m, 8 Nov. 1977, *G.T. Prance & al. 25017* (MO, US); Oriximinà, along Rio Trombetas, ca. 8–10 km SE from Cachoeira Portiera, 29 Jun. 1980, *C. Davidson & G. Martinelli 10580* (MO, NY); Sete Varas airstrip on Rio Curua, 54°92'W, 0°95'S, 5 Aug. 1981, *J.J. Strudwick & al. 4176* (MO, NY, US); Serra dos Carajás, 6°03'S, 50°16'W, 650 m, 19 May 1982, *C.R. Sperling & al. 5771* (K, MO, NY, US); Marabá, mata de Cipó, 24 May 1982, *R.S. Secco & al. 331* (K, MO, NY, US); **Paranà**. 1857, *R. Spruce 1099* (K, US, W); Alexandra, 5 Mar. 1911, *P. Dusén 11487* (MO, US); Condrina, 6–8 Mar. 1946, *J.R. Swallen 8756* (US); Campo Morao, 28 Mar.–2 Apr. 1946, *J.R. Swallen 9005* (MO, NY, US); Antonina, Pinheirinho, 22 Mar. 1966, *G. Hatschbach 14091* (K. US); 15 km E of São Tomé, 220 m, 5 Apr. 1966, *J.C. Lindeman & J.H. de Haas 929* (K, US, W); **Pernambuco**. Garunhuns, 450 m, 26–27 Nov. 1924, *A. Chase 7833* (MO, US); W of Recife, 21 Jul. 1967, *J.C. Lindeman & J.H. de Haas 6198* (NY); Caruarú, Serra dos Cavalos, 15 Sep. 1981, *A. Ferreira 125* (K, MO, US); Caruarú, Murici, Brejo dos Cavalos, Parque Ecologico Municipal, solo arenoso, 1100 m, 08°18'36"S, 36°00'00"W, 10 Sep. 1994, *S. Mayo & al. 1024* (K, MO, NY, US); Caruaru, Distr. Murici, Brejo dos Cavalos, 4 Sep. 1995, *R.P.* de *Oliveira 66* (K); Reserva Biológica da Pedra Talhada, Lagoa do Ouro, 28 Oct. 2014, *L. Nusbaumer 4257* (G); **Rio de Janeiro**. Mandiocca, s.d., *G. von Langsdorff 405* (G, UPS); Rio de Janeiro, 1817–1818, *G. Raddi s.n.* (FI, PI); Rio de Janeiro, 1833, *M. Gaudichaud 303 bis* (G, P); Corcovado, 1840, *M. Guillemin 826* (G, P); Rio de Janeiro, Mar. 1872, *A. Glaziou 1007* (BM, C, FI, NY, K, P, US); Corcovado, 25 Apr. 1887, *J. Schenk 3754* (C); Rio de Janeiro, bei Palmeiras, Apr. 1900, *E. Ule 4993* (L); Corcovado, 8 May 1925, *A. Chase 9744* (MO, NY, US); Rio de Janeiro, Pao de Assicar, vicinity of Rio de Janeiro, 15 May 1925, *A. Chase 9796* (US); Rio de Janeiro, Meio da Serra, 500 m, 22°33'S, 43°11'W, 7 Apr. 1929, *L.B. Smith & A.C. Brade 2284* (BM, NY, P, US); Restinga de Jacarepaguá, 17 Apr. 1940, *B. Lutz 1374* (BM); Guanabara, Gavea, São Conrado, May 1960, *A.P. Duarte 5221* (MO, US); Rio de Janeiro, Inoa, 300 m, 23 Jul. 1961, *L. Emygdio &*

B. Marx 1217 (US); Guanabara, Tijuca, 19 Apr. 1963, *J.P. Lanna 568* (NY); Rio de Janeiro, Ilha de Paquetá, 11 May 1993, *M.G. Bovini 104* (HUEFS); City of Paratí, 23°13'S, 44°21'W, 21 Apr. 1965, *G. Eiten & L.T. Eiten 6279* (MO, US); Marambia, entrada Niteroi-Friburgo, 25 May 1965, *F.C. Hoehne 5998* (US); Rio de Janeiro, Guanabara, Alto da Boa Vista, 6 Jan. 1968, *D. Sucre 2098* (MO, US); E da Guanabara, Serra da Mendanha, 9 Apr. 1970, *D. Sucre 6555* (G, MO, US); Estrada Velha, Rio de Janeiro-Petrópolis, Mata do Principe, 6 Mar. 1972, *T.R. Soderstrom & D. Sucre 1872* (K, L, MO); Serra da Mendanha, forest on P.H. Gentle slopes, consisting of palms, bamboos (*Bambusa*, *Chusquea*, *Merostachys*), *Pharus* spp., *Olyra* sp., and mostly small trees, 19 Apr. 1972, *T.R. Soderstrom & D. Sucre 1948* (K, MO); Between Cachoeira de Macacu and Nova Friburgo, 280 m, 29 Apr. 1972, *T.R. Soderstrom & D. Sucre 1976* (MO); Santa Alice, Itaguai, 10-15 m, 17 May 1978, *K. Mizoguchi 602* (MO); Niteroi, Praia de Itaipuçu, Alto Moinas, 100-250 m, 22°53'S, 43°07'W, 1 Jul. 1982, *T.B. Croat 53744* (MO); Angras dos Reis, Ilha Grande, Reserva Biológica Estadual da Praia do Sul, 23°10'S, 44°17'W, 11 Apr. 1984, *D. Araujo & al. 6201* (K); Resende, Parque Nacional de Itatiaia, Rio Campo Belo, proximo de Cachoeira Véu Nova, 1150 m, 30 Apr. 1985, *F.O. Zuloaga 2368* (MO, US); **Rio Grande do Sul**. Santo Angelo et Silveira Martins, 2 Mar. 1893, *C.A.M. Lindmann 1239* (UPS); **Rondônia**. Vicinity of Jaciparaná, on road WNW of village, 24 Jun. 1968, *G.T. Prance & al. 5158* (K, MO, NY, US); Basin of Rio Madeira, 3 km W of Rio Madeira along road Abunã to Rio Branco, 13 Jul. 1968, *G.T. Prance & al. 5954* (K, MO, NY, US, P); Basin of Rio Madeira, 1 km N of Riberão, road Abunã-Guajará-Mirim, 25 Jul. 1968, *G.T. Prance & al. 6451* (C, K, MO, US, NY); Basin of Rio Madeira, vicinity of São Lorenço mines, 65°6'W, 9°33'W, 27 Nov. 1968, *G.T. Prance & al. 8926* (K, MO, NY, US, P); Ariquemes, Mineração Mibrasa, Setor Alto Candeias, 10°35'S, 63°35'W, 11 May 1982, *L.O.A. Teixeira & al. 104.091* (K, NY, US); Santa Barbara, Rodovia BR 364, 9°10'S, 63°07'W, 28 May 1982, *L.O.A. Teixeira & al. 104565* (K, NY, US); Ca. 2 Km ENE along road to São Sebastiao off BR-364, 23 May 1984, *D. Frame & al. 139* (MO, US); Rondônia, Rolin de Moura, estrada para Brasilandia, 11°12'S, 61°62'W, 18 Jun. 1984, *C.A. Cid & al. 4624* (K, MO, NY); **Roraima**. Porto Velho, Territorio do Guaporé, 24 May 1952, *G.A. Black & E. Cordeiro 52-14444* (P); Base of Serra Tepequem, Boca de Mata, 11 Feb. 1967, *G.T. Prance & al. 4311* (K, MO, NY, US); Porto Velho, Rio Jaci-Paraná, Jirau-Porto Velho, 09°16'19"S, 64°23'37"W, 89 m, 27 Jun. 2012, *M.F. Simon et al. 1564* (NY); Jaci Paraná, Ro Jaci Paraná, 9°16'18"S, 64°23'37"W, 89 m, 27 May 2014, *N.A. Perogolo et al. 365* (NY); **Santa Catarina**. Brusque, Azambuja, Brusque, 35-135 m, 27°06'S, 48°54'W, 4 Mar. 1952, *L.B. Smith & R. Reitz 6039* (US); Itapaì, morro da Fazenda, 4 Mar. 1954, *P.R. Reitz & R. M. Klein 8292* (G); **São Paulo**. São Paulo, Municipio de Iepê, fazenda C.A.P.I., 4 km N of the Rio Paranapanema & 6 km E of Porto Alvorada, 300 m, 22°44'S, 51°71'W, 9 Feb. 1965, *G. Eiten & L.T. Eiten 5955A* (K, NY, US); Bocaina do Sul, Guará, São José, 29 Mar. 1997, *R.M. Harley 28543* (CEPEC, HUEFS); Paraty, lado opposto da Cachoeira do Promirim, 23°22'33"S, 44°57'55"W, 8 Jun. 2006, *M.M. Silva-Castro 1027* (HUEFS).

COLOMBIA. Antioquia. San Luis Cañon del Rio Claro, 325-400 m, 05°53'N, 74°39'W, 7 Mar. 1984, *A. Cogollo 1413* (MO); **Caquetá**. Montañita ad flumen Rio Orteguaza, 2 Aug. 1926, *G.J.N. Woronow & S. Juzpepczuk 6379* (US); On road from Florencia to Neiva (near Sucre), 1080 m, 24 Jan. 1969, *T.R. Soderstrom 1415* (K, MO, NY, US), ***n* = 18!** (Gould and Soderstrom 1970); **Cauca**. El Tambo, 25 Jul. 1934, *K. von Sneidern 164* (G); Parque Nacional Munchique, El Tambo, vereda La Romelia, la Gallera, 24 Jul. 1993, *F. González & al. FG 2813* (MA); El Tambo, vereda La Romelia, camino de Nueva Grenada, 28 Jul. 1993, *M. Velayos & al. MV7033* (MA). **Cundinamarca**. South side of guaivo River, 28 km NE of Gachalà, Puerto Rico, 1660 m, 31 Oct. 1944, *M.L. Grant 10549* (NY, US); Río Loretoyacu, Oct. 1946, *G.A. Black 46-185* (K); **El Valle**. Cordillera Occidental, entre San Antonio y Mares, 14 Nov. 1943, *J. Cuatrecasas 15202* (G); Bosque de San Antonio, W of Cali, near TV tower, 1950-2050 m, 15 Jul. 1984, *A. Gentry 48146* (MO); **Mariquita**. Cauca, Quindio, 2000 m, Jul. 1853, *J. Triana s.n.* (US); **Tolima**. Andes, Cordillera Central, Ibaqué, bosque y matarral, 8 May 1932, *J. Cuatrecasas 2995* (MA).

DOMINICAN REPUBLIC. Liali. Liali, 100-500 m, 9 Feb. 1923, *W.L. Abbott 2597* (US); **Maria Trinidad Sánchez**. Rio San Juan, 18 Mar. 1928, *G.S. Miller 1184* (US); **Samaná**. Vicinity of Sanchez, Samaná Peninsula, 0-300 m, 3 Dec. 1920, *W.L. Abbott 121* (US); **Vega**. Vicinity of Pedra Blanca, 200-500 m, 14 Nov. 1945, *H.A. Allard 13333* (US); La Vega, vicinity of Pietra Blanca, 200-500 m, 10 Dec. 1947, *H.A. Allard 17779, 17785* (US).

ECUADOR. **Los Rios (or Pichinga)**. At El Centinala at crest of Montanas de Ila road from Patricia Pilar to 24 de Mayo at km 12, 600 m, 7-12 Feb. 1979, *C.H. Dodson & J.A. Duke 7666* (US); **Madre de Dios**. Manu, Puerto Maldonado, Los Amigos Biological Station, Madre de Dios River, ca. 7.0 km upriver from mouth of Río Los Amigos, 270 m, 12°57'S, 70°01'W, 22 May 2001, *J.P. Janovec & al. 2206* (MO); **Morona-Santiago**. Taisha, path running along pastures near the military camp, 444 m, 77°30'W, 02°23'S, 21 Jun. 1980, *J. Brandbyge 32136* (K, US); Morona Santiago, Los alrededores del Centro Tuutin Entsa, 330 m, 12 Aug. 1985, *L. Ananch 101* (MO); **Napo**. Napo-Pastaza, near Tena, 400 m, 2-11 Apr. 1935, *Y. Mexia 7218* (BM, US); Santa Cecilia, 340 m, 30 Mar. 1972, *J.D. Dwyer & J.E. Simmons 9753* (MO); North shore of the Yasuni River not too far from the Napo River, at the edge of a clearing in tropical rain forest, 270 m, 25 Aug. 1979, *S.M. Young 23* (US); Río Eno near San Pablo at Río Agarico, 250 m, 76°31'W, 00°11'S, 20 Feb. 1984, *S. Lægaard 51503* (K, MO, NY, UPS); Río Napo below Mishauali, 14-15 Dec. 1985, *S. Lægaard 55837* (K); Río Napo, 8 km al E de Mishauali, 450 m, 01°04'S, 77°36'W, 24 Apr.-5 May 1987, *C.E. Cerón 1355* (MO, NY); Orellana Canton, Parque Nacional Sumaco Napo-Galeras, zona de amortiguamiento fuera del parque, Comunidad Mushullacta a 1.2 km al E del Río Punino, 425 m, 00°12'S, 77°16'W, 18 Oct. 1996, *H. Vargas & A. Alvarado 1051* (MO); Napo, Cotococha, about 1 km W of Venecia, S side of the Napo River, 450 m, 01°3.088'S, 77°42.72'W, 13 Jun. 2003, *L.R. Landrum 10611* (MO, NY); **Pastaza**. Tungurahua, valley of Pastaza River etween Banos and Cashurco, 8 hours east of Banos, 1300-1800 m, 25 Sep. 1923, *A.S. Hitchcock 21863* (US); Río Ishpingo, tributare of Río Pastaza, 285 m, 76°45'W, 02°25'S, 22 Jul. 1980, *B. Øllgaard 35024* (K, US); **Zamora-Chincipe**. Zamora, ca. 15 km W of Zumba, 27 Apr. 1992, *S. Lægaard 102469* (K); El Oso, km 40 Loja-Zamora, 04°00'S, 79°02'W, 21 Jun. 1998, *S. Lægaard 18927* (K, MO).

FRENCH GUIANA. La Mana, s.d., *P.A. Sagot 656* (G, NY, P, W); 1840, *F.M.R. Leprieur s.n.* (FI-Webb, G, L, P); s.l., 1842, *M. Mélinon s.n.* (L, P, US); Vicinity of Cayenne, 4 Jun. 1921, *W.E. Broadway 415* (NY); Cayenne-route du Mohury, 2 Jul. 1955, *J. Hoock 82* (K, NY, P); Cayenne, chemin du moulin Vidal, 13 Jul. 1955, *J. Hoock 89* (CAY, K, P, US), 14 Jul. 1955, *J. Hoock 90* (NY, US); Cayenne, 2 Jul. 1956, *J. Hoock s.n.* (P); Près de Maripasoule, 1 Sep. 1961, *R.A.A. Schnell 11692* (P, US); Manoi, 24 Aug. 1962, *J. Hoock 93* (CAY, G, MO, NY, P); Cayenne, route de Stoupan, 21 Jul. 1970, *R.A.A. Oldeman B-3485* (P, US); Tumuc Humac, frontière Brésil-Guyane, 500 m, 25 Aug. 1972, *J.J. de Granville 1380* (CAY, P, US); Camopi, Trois-Sauts, 7 Sept. 1976, *P. Allain PA69* (P); Saül, rudérale dans la village, 15 Sep. 1979, *M.F. Prévost 787* (CAY); Cayenne, Montravel, 8 Apr. 1982, *G. Cremers 7761* (CAY, MO, P); Haute Canopi, Mont Belvédère, 23 Nov. 1984, *J.J. de Granville 6982* (CAY, MO, P); Haut Oyapock, village Zidock, 20 Aug. 1985, *M.F. Prévost & Grenand 1969* (K, P); Saül Region, along road between airport and Saül, 200 m, 3°37'N, 53°12'W, 29 Oct. 1986, *L. Skog & C. Feuillet 7106* (SD, US); Ile de Cayenne, Mont Baduel, 20 m, 52°19'W, 4°55'N, 23 May 1987, *M. Hoff 5199* (CAY, P, US); Saül, 300 m, 3°40'N, 53°10'W, 28 Jul. 1987, *W. Hahn 3663* (CAY, NY, P, US); Bassin du Haut Marouini, Roche Koutou, 320 m, 54°4'W, 2°52'N, 16 Aug. 1987, *J.J. de Granville & al. 9320* (MO, US); Ile de Cayenne, Mont Cabassou, 40 m, 6 Oct. 1989, *M. Hoff 5694* (CAY, G, MO, NY, P, US); Saül, vicinity of Eaux Claires, on the route de Bélizon, 0-4 km S of Eaux Claires, 200 m, 3°37'N, 53°12'W, 11 Oct. 1991, *S. Mori & al. 22086* (MO, US); Ile de Cayenne, Mont Rorota, 20 m, 52°15'W, 4°53'N, 1 Apr. 1994, *B. Bordenave 901* (P, US); Ile de Cayenne, Mont Grand Matoury, 5 Apr. 1995, *G. Cremers & al. 13869* (CAY, MO, P); Bassin de l'Oyapock, Roche Touatou, 120 m, 19 May 1995, *G. Cremers & J.J. de Granville 14008* (CAY, G, NY, P, US); Roche Touatou, Bassin de l'Oyapock, 120 m, 52°32'N, 2°57'W, 23 May 1995, *J.J. de Granville & G. Cremers 13048* (P, US); Savane Renner, Région littorale, 52°53'N, 5°20'W, 3 m, 1996, *G. Cremers & J.J. de Granville 14455* (CAY); Region de Saül, 220 m, 53°13'W, 3°28'N, 3 Apr. 1997, *G. Cremers & F. Crozier 14636* (P, MO, US); Taluwen (Apoya) abatti wayana, 9 Nov. 1997, *M. Pignal 1502* (NY); Region de Saül, 53°13'W, 03°28'N, Montagne Trésor, le long route de Kaw, Roura, 21 Nov. 1997, *Rouselle GU96/106* (MA); Montagne Favard, au sommet de la colline, 4°52'N, 52°2'W, 5 Nov. 1998, *O. Poncy & F. Crozier 1128* (CAY, NY, P); Maripasoula, 54°3'W, 3°40'N, 3 Nov. 1999, *M. Fleury 1581* (CAY); Pic Matécho, versant sud, 450 m, 53°2'N, 3°44'W, 19 Sep. 2000, *J.J. de Granville & al. 14294* (CAY, NY, US); Monts d'Arawa, savane-roche centrale, 53°22'00"N, 02°49'00"W, 11 Jul. 2002, *J.J. de Granville & al. 15207* (CAY, MO, NY); Inselbergs de la haute Wanapi, 170 m, 53°49'20"W, 2°31'00"N, 13 Apr. 2004, *J.J. de Granville & al. 15880* (CAY, MO, US); Inselbergs du haut Marouini, inselberg de la D.Z., 190 m, 2°36'30"N, 54°1'45"W, 21 Jun. 2004, *J.J. Granville & F. de Crozier 16318* (CAY, MO, US); Inselbergs du haut Marouini, 200 m, 2°36'20"N, 54°40"W, 27 Jun. 2004, *J.J. Granville & F. de Crozier 16487* (CAY, MO, US); Cayenne, colline Montabo, 4 m, 25 Nov. 2005, *C. Girod 3159* (CAY); Kaw Mts., Trésor Reserve, 210 m, 4°35'N, 52°17'W, 2 Oct. 2006, *M.J. Jansen Jacobs & al. 1812* (US); Site Ariane 4–Crique Karoubo, 8 m, 05°14'18"N, 52°47'52"W, 11 May 2007, *J.J. de Granville & O. Tostain 17393* (CAY, US); Saül, aval Crique Cambrouze, 200 m, 03°36'16"N, 53°14'43"W, 11 Feb. 2008, *O. Tostain & al. 1683* (CAY, US); ZNIEFF Abattis Kotika, 61 m, 04°1'20.7"N, 54°19'14.9W, 6-17 Sep. 2011, *G. Quenette 35* (CAY); Maripasoula, massif du Mitaraka, Crique Alama Sommet en Cloche, flanc nord den contrebas du dôme, 2°13'50"N, 54°28'W, 9 Mar. 2015, *O. Poncy 2890* (CAY); Commune de Cayenne, Sentiere de Montabo, 4°56'41"N, 52°19'03" W, 10 m, 28 May 2022, *R.M. Baldini 2118, 2119, 2121* (CAY, FT).

GUYANA. Barina-Waini. Aruka River, Oct. 1905, *H.H. Bartlett 8576* (K, US); Aruka River, 8°10'N, 59°50'W, 16 Jan. 1920, *A.S. Hitchcock 17553* (BM, C, G, K, L, MO, NY, P, US, W); Waini River, NW Distr., 3-18 Apr. 1923, *J.S. De La Cruz 3663* (K, MO, NY, US); Assakatta, NW Distr., 7°45'N, 59°5'W, 18-28 Sep. 1923, *J.S. De La Cruz 4291* (K, MO, NY, US); Barima-Waini Region: Aranka Head, 107 m, 7°25'N, 60°32'W, 10 Apr. 1991, *T. McDowell 4365* (CAY, K, MO, US); **Berbice-Corentyne**. Corentyne River, Sep. 1879, *G.S. Jenman 257* (K); Berbice River, Dec. 1886, *G.S. Jenman 3593* (K, NY); Baba Grant Sawmill, Corentyne River above Cow Falls, 5°00'N, 57°42'W, 10-25 m, 21 Apr. 1990, *T. McDowell 2424* (NY, US); **Cuyuni-Mazaruni**. Near Bartica, Jul. 1884, *G.S. Jenman 2053* (K); Upper Mazaruni River region, between Kako and Akawaio Indian village on the Kako river near its junction with the Maxaruni River and Karowtipu, 500 m, 5°45'N, 60°35'W, 15 Apr. 1987, *B. Boom & D. Gopaul 7332* (MO, NY, US); **Essequibo Islands-W Demerara**. Naamryck Canal, ca. 8 km SE of Naamryck Public Road, just W of Lookout Village, 1 m, 6°50'N, 58°25'W, 31 Mar. 1988, *J.J. Pipoly 11301* (CAY, MO, NY, US); **Pomeroon-Supenaan**. Pomeroon River, Dec. 1886, *G.S. Jenman 1916* (K); **Potaro-Siparuni**. Second-growth thickets along Potaro River, Tumatumari, Jun.-Jul. 1921, *H.A. Gleason 70* (K, NY, US); Chenapou, Amerindian village (Patumona), 50 km upstream from Kaieteur Falls, 450 m, 5°00'N, 59°34'W, 16 Oct. 1987, *L.P. Kvist 305* (CAY, K, MO, US); Pakaraima Mts., upper Ireng River, 15-20 km up river from Cipo settlement, Julong Falls, 05°00'N, 59°57'W, 701 m, 2 Nov. 1994, *P. Mutchnick 354* (CAY, MO, US); Mt. Kopinang, 1500-1600 m, 4°58'N, 59°53'W, 7 Apr. 1988, *W. Hahn 4349* (NY, US); Nyion, trail from Kato to Paramakatoi, 650 m, 4°40'N, 59°50'W, 12 Mar. 1989, *W. Hahn 5634* (CAY, MO, NY, P, US); Micobe, 200 m, 59°30'W, 05°20'N, 20 Oct. 1991, *S. Tiwari 462* (MO, NY); Pakaraima Mts., Cipo Mt., ca. 2 km from summit escarpment, headwaters Cipo Creek, 1000 m, 04°54'N, 60°05'W, 26 Jan. 1993, *T.W. Henkel 967* (US); Garraway stream, 102,5 miles on Bartica-Potaro Road, 38 m, 5°22'25.2"N, 59°7'20,5"W, 12 Mar. 2004, *K.M. Redden 2184* (US); **Rupununi**. Rupununi River, Isherton, 9-15 Nov. 1937, *H.H. Smith 2417* (K, NY, US); Marudi Mts., ca. 1 km along trail from Nor Man Mines camp to Aishalton, 300-400 m, 02°15'N, 059°10'W, 9 Nov. 1982, *A.L. Stoffers & al. 238* (K, MO, NY, US); Between Kuyuwini Landing and Kassikaityu River, 150-250 m, 02°00'N, 059°15'W, 18 Oct. 1992, *M.J. Jansen-Jacobs & al. 2989* (CAY, MO, NY, P, US); Kuyuwini Landing and Kassikaityu River, 150-250 m, 02°05'N, 059°15'W, 30 Oct. 1992, *M.J. Jansen-Jacob & al. 3176* (CAY, MO, NY, P, US); **Upper Demerara-Berbice**. Upper Demerara River, Sep. 1887, *G.S. Jenman 4089* (K, US); **Upper Takutu-Upper Essequibo**. Surama Village, headed ca. 4 km NW of village, ca. 10 km N of new Paranapanum Rd., 60-90 m, 4°08'N, 59°04'W, 19 Feb. 1990, *T. McDowell 1889* (FT, US); Acarai Mts., Tinarnau Creek at NW base of Tirarnau Peak, 500 m, 01°16'N, 58°36'W, 5 Mar. 1994, *T.W. Henkel 4940 pro parte* (US); Rewa River, 0,5 km S of Great Falls, 03°10'N, 58°40'W, 90 m, 20 Sep. 1997, *D. Clarke 6666* (US); Wassarai Mts., 01°35'57"N, 059°14'17"W, 27 Aug. 1999, *D. Clarke 7997* (CAY, NY); Wassarai Mts., summit of unnamed peak, 10.5 km S of Kassikaityu R., 900 m, 01°33'10"N, 059°14'35"W, 15 Sep. 1999, *D. Clarke 8637* (US); Rewa River, Spider Mts., 03°08'N, 05°32'W, 16 Sep. 1999, *M.J. Jansen-Jacobs & al. 5930,* 23 Sep. 1999, *M.J. Jansen-Jacobs & al. 6099* (CAY, K, MO, NY).

LEEWARD ISLANDS. **St. Croix.** Propserity Garden, 5 Jan. 1906, *C. Raunkiaer 642* (C); **St. Kitts**. s.d., *Walsh s.n.* (K); **St. Thomas**. St. Thomas, 1802, *Ventenat s.n.* (BM); 11 Dec. 1905, *C. Raunkiaer 2304* (C); St. Thomas, St. Peter, 11-22 Feb. 1913, *E.G. Britton & D.W. Marble 1230* (NY, US); St. Thomas, Water Island, 3 Jan. 1914, *C.H. Ostenfeld 55 p.p.* (C).

PARAGUAY. Amambay, Bella Vista, 14 May 1986, *F. Mereles 619* (G); Guairá, Tororò, subida al Cerro Acate, 20 Jan. 1988, *I. Basualdo 1399* (G).

PERU. Amazonas. Bongará, 5km SE of Yambrasbamba, 2100-2400, 25 Jun. 1962, *J.J. Wurdack 1048* (K, NY, US); Bongará, lower portion of Shipasbamba-Pomacocha trail, 1600-1900 m, 29 Jun. 1962, *J.J. Wurdack 1096* (K, NY, US); Bagua, Valley of Río Marañón above Cascadas near Campamento STe. Montenegro, 450 m, 3-4 Sep. 1962, *J.J. Wurdack 1807* (K, NY, P, US); Amazonas, Quebrada Huampami, Río Cenepa, 890 ft, 8 Jun. 1973, *R. Kayap 903* (K, MO); Amazonas, Bagua Prov., Distr. Imaza, Region NE del Marañon, Comunidad de Yamayakat, Río Marañon, 320 m, 04°55'S, 78°19'W, 14 Jul. 1994, *R. Vasquez & al. 18647* (MO); Prov. Bagua, Distr. Imaza, Comunidad Aquaruna Yamayakat, Camino hacia Temashnum, 300-480 m, 17 Aug. 1996, *C. Diaz & al. 7905* (MO); **Ayacucho**. Estrella, between quanta and Río Apurimac, 500 m, 8-14 May 1929, *E.P. Killip & A.C. Smith 23080* (NY, US); **Cajamarca**. San Ignacio, Distr. Huarango, Caserio El Triunfo, Fundo El Convento, 2100 m, 05°13'S, 78°40'W, 1 Jul. 1996, *E. Rodriguez R. 1244* (MO); Cutervo, 5 km N of Santo Domingo de la Capilla on road towards Chiple, 22 Mar. 2000, *P.M. Peterson & N. Refulio Rodriguez 15034* (K); **Cuczo**. Paucartambo, Hacienda Villa Carmen, 540 m, 19 Jul. 1963, *C. Vargas 14689* (US); Prov. Quispicanchi, Distr. Camanti, Maniri, 8 km W de Quincemil, 720 m, 13°17'S, 70°48'W, 22 Jul. 1990, *M. Timaná & H. Astete 712* (M); Distr. Echarate, Palma Real, Koribeni, 718 m, 1280'30"S, 7249'45"W, 16 Jul. 2007, *G. Calatayud & al. 4342* (MO); **Huanuco**. Tingo Maria, Valley of Río Huallaga, 7000 ft, 11-14 Jul. 1937, *C.M. Belshaw 3086* (K, MO, NY, P, US); Alrededores de Tingo Maria, 700 m, 11 Aug. 1946, *R. Ferreyra 920* (US); Vicinity of Tingo Maria, 22 Jun. 1959, *M.E. Mathias & D. Taylor 3463* (K); Pachitea, Honoris, Bosque Nacional de Iparia, 8 May 1967, *J. Schunke Vigo 1938* (K, P, MO, US); Prov. Leoncio Prado, Distr. Rupa Rupa, al E de Tingo Maria, cerca al Cerro Quemado, 672-800 m, 5 Apr. 1978, *J. Schunke Vigo 10089* (MO); **Loreto**. Pinto-Cocha on the Río Nanay, Jun. 1929, *L.O. Williams 399, 781* (K, US); Iquitos, 3-11 Aug. 1929, *E.P. Killip & A.C. Smith 27125* (MA, NY, US); Yurimaguas, lowe Río Huallaga, 135 m, 22 Aug.-9 Sep. 1929, *E.P. Killip & H.H. Smith 27561* (MA, NY, US); Iquitos, 120 m, Oct. 1929, *L.O. Williams 3717* (G, US); Vicinity of Iquitos, San Juan, 7 Nov. 1940, *E. Asplund 14378* (G, K, NY, UPS, US); About 3 km S of Yurimaguas on Río Shanusi, 180 m, 1 Jun. 1964, *R.M. Straw 2450* (US); Prov. Coronel Portello, Dept. Iparia, Bosque Nacional de Iparia, 18 Aug. 1968, *J. Schunke Vigo 2618* (G, NY, US); Valseci-Rudolpho, Río Corrientes between Q. Platanoyacu and mouth of Río Macusari, 18 Sep. 1968, *S. McDaniel 11097* (NY); Alto Amazonas, Lagunas, trail to Argentina, 6 Jul. 1972, *S. McDaniel & M. Rimachi 16411* (MO, NY); Alto Amazonas, Yurimaguas, lower Río Paranapura, partially disturbed forest, 180 m, 9 Jul. 1972, *S. McDaniel 16566* (MO, US); Maynas, Quebrada Tahuayo above Tamishiyaco, 27 Aug. 1972, *T.B. Croat 19761* (K, L, MO); Altura Tuta Pischco on Río Napo, 16 Sep. 1972, *T.B. Croat 20302* (L); Vicinity of Aguaytia, primary forest on steep slopes along Río Aguaytia, 3 Oct. 1972, *T.B. Croat 21008* (MO); Rio Ampiyacu, Pebas and vicinity, 71°49'W, 3°10'S, 4 May 1977, *T.C. Plowman & al. 7251* (K, US); Maynas Iquitos, carretera de Zingaro Cocha, 150 m, 1 Sep. 1981, *M. Rimachi 5634* (NY, US); Requena, restinga del Capite, abajo de S. Herrera, Río Ucayali, 26 Aug. 1982, *F. Encarnación 26216* (G, MO); **Madre de Dios**. Cocha Cashu, forest in vicinity of Lake of Río Manu, between Panagua & Tayakome, 17-24 Aug. 1974, *R.B. Foster 3487* (MO, US); Rio Manu, Cocha Cashu station, 350 m, 23 Jul. 1979, *R.B. Foster & al. 6832* (F); Tambopata, Tamponata Nature Reserve, 260 m, 12°49'S, 69°17'W, 30 May 1980, *P.J. Barbour 5432* (MO, NY); 30 km SW from Pto. Maldonado, 12°50'S, 69°20'W, 6 Sep. 1985, *X. Londoño 14* (MO, US); 39 km SW of Puerto Maldonado, near the confluence of Río Tampopata and Río La Torre, 12°50'S, 69°20'W, 7 Jul. 1987, *H.H. Smith & al. 909* (K, L, MO, NY, US); Tambopata, 280 m, 12°49'S, 89°18'W, 11 Aug. 1990, *C. Reynel & E. Meneses 5032* (MO); Parque Nacional Manu, Río Manu, Pakitza, Radial 3, a 0,4 km de la trocha Tachigali, 330 m, 11°56'S, 71°15'W, 24 Apr. 1991, *X. Londoño 616* (US); Manu, Centro de Investigacion y Capacitacion Rio Amigos, 250 m, 12°55'.90"S, 70°08'.87"W, 24 Sep. 2003, *J. Oliver 2* (P); **Pasco**. Oxapampa, Río Palcazu valley, Río San José, in the Río Chuchuras drainage, 400-500 m, 75°20'W, 10°10'S, 14 May 1983, *D.N. Smith & E. Palanchak 4026* (MO, US); Oxapampa, Río Huaylamayo, Ancahuachanan SW of Chorobamba, 1850 m, 4 May 1984, *D.N. Smith 6991* (MO); Oxapampa, Villa Rica, Comunidad Nativa San Pedro de Pichanaz, sector San Francisco de Pichanaz-Albergue turistico COROP, 518 m, 10°30'03"S, 75°04'14"W, 9 Jun. 2008, *R. Rojas & al. 5738* (MO); **Jaen**. Tiruyas, 30 km from Huancabamba, valley of Río Tabaconas, 1600 m, 11 Jun. 1947, *F.R. Fosberg 27757* (MO, US); **Junín**. Río Paucartambo Valley, near Perene Bridge, 19 Jun. 1929, *E.P. Killip & A.C. Smith 25255* (NY, US); Puerto Yessup, 10-12 Jul. 1929, *E.P. Killip & A.C. Smith 26327* (NY, P); Tarma, 9 km SW of San Ramon, 1500 m, 4 Dec. 1962, *H.H. Iltis & al. 313* (K, US); San Francisco de Satipo, 700 m, 23 Jun. 1977, *J.C. Solomon 3240* (MO); Chanchamayo, La Merced-Puente Paucartambo road, near San Luis Shuaro, 780 m, 75°19'W, 10°55'S, 17 May 1983, *H.H. Smith 4071* (K, MO, US); Satipo, along road between La Merced and Satipo, 1000 m, 11°10'S, 74°39'W, 8 Jun. 1998, *T.B. Croat & M. Sizemore 81977* (MO); **San Martín**. Along Río Curiyacu, an affluent of Río Cumbasa, about 8 km above San Antonio, 1400 ft, 7 Nov. 1937, *C.M. Belshaw 3615* (P, US); Arriba de San José de Sisa, 500–550 m, 21 Jul. 1950, *R. Ferreira 7916* (US); At 25 km on road to Lima from Tingo Maria along Huallaga Road, 750 m, 30 Oct. 1949-19 Feb. 1950, *H.A. Allard 21524* (NY, US); Saposoa, 450 m, 13 Jul. 1964, *F. Woytkowski 8349* (MO); Mariscal Cáceres, Distr. Tocche Nuevo, Fondo Miramar, 450 m, 3 Jul. 1978, *J. Schunke Vigo 7559* (K, US); Tarapoto, carretera Tarapoto-Yurimaguas, 700 m, 14 Jun. 1980, *M. Rimachi 5155* (MO, NY); Mariscal Caceres, Distr. Tocache Nuevo, Río de La Plata, fundo del Sr. Manuel Gatica, 550-700 m, al borde de la quebrada, en bosque alto, 12 Aug. 1980, *J. Schunke Vigo 12146* (US); 36 km NE of Tarapoto, Río Cainarachi, 6°20'S, 76°20'W, 22 Jul. 1982, *A. Gentry & al. 37939* (G, NY); **Uyacali**. Coronel Portillo, Bosque Nacional de von Humboldt, km 86, Pucallpa-Tingo Maria road, 270 m, 08°40'S, 75°00'W, 7 Aug. 1980, *A. Gentry & A. Salazar 29418* (MO); Coronel Portillo, Yarinacocha, quebrada Maputay, 8°21'S, 74°34'W, ca. 200 m, 24 Jul. 1998, *J. Graham & J. Schunke Vigo 516* (F); Purus, Río Curanja, cerca la Comunidad nativa colombiana, 300-350 m, 10°04'S, 71°06'W, 9 Jul. 2002, *J.G. Graham & J. Schunke Vigo 16158* (MO); Padre Abad, Carretera al caserio San Miguel y Mapuya, 12 a 17 km de la Aguaytia, 9°05'S, 75°26'W, 350 m, 10 Jan 2004, *J. Schunke Vigo & J.G. Graham 16181* (G).

PUERTO RICO. Porto Rico, s.d., *C. Bertero s.n.* (TO); 1827, *H. Wydler 250* (FI-Webb, G); Puerto Rico, Dec. 1883, *A. Stahl 7* (W); Maricao, 13 Nov. 1884, *P.E.E. Sintenis 215* (BM, K, NY, US, W); Prope Lares in fruticetis ad "Palina Llanos", 17 Jan. 1887, *P.E.E. Sintenis 5918* (C, US); Luquillo Mountains, Jul. 1902, *P. Wilson 350* (NY, US); Vicinity of Mayagüez, 4-10 Mar. 1906, *E.G. Britton & D.W. Marble 678* (NY, US); Vicinity of Arecibo, 8 Nov. 1913, *A. Chase 6454* (US); Jajome Alto, vicinity of Cayey, 3 Dec. 1913, *A. Chase 6747* (L, US); Near Maricao, Indiera Fria, 19-22 Feb. 1915, *N.L. Britton & al. 4490* (K, NY, US); Guavate State Forest, 14 Dec. 1963, *A.H. Liogier 10418* (NY, US); In forest from Mayagüez to Maricao, 25 Feb. 1982, *A.H. Liogier & al. 32736* (NY); Cayey, Cerro Avispa, 10 Feb. 1983, *A.H. Liogier & L.F. Mar-*

torell 33832 (NY); Maricao State Forest, 15 Jan. 1986, *A.H. Liogier 35847* (NY); Caribbean National Forest, along Highway 966, ca. 0.5 km E of Junction with Highway 191, 450-500 m, 18°17'N, 65°47'W, 5 Jan. 1987, *B.M. Broom 6911* (MO, NY, US); Maricao, Bairro Maricao Afuera, Rio Maricao margins, 18°10'16"N, 66°59'17"W, 10 Feb. 1994, *J.A. Cedeño 238* (NY).

SURINAME. *F.W. Hostmann 13* (G, K), *F.W. Hostmann 511* (G); In fruticetis Surinami, prope Lustryk, 30 Dec. 1837, *Splitgerber 446* (L); 1827, *C. Weigelt s.n.* (FI-Webb, G, L, MO, W); 1842, *C.V. Hartmann 13* (FI-Webb); In distr. Para, Feb.-Apr. 1844, *A. Kappler s.n.* (G, K, W); Sandrij, 14-25 Nov. 1934, *W.A. Archer 2759* (K, US); Charlesburg Rift, 3 km N of Paramaribo, 5 Apr. 1944, *B. Maguire & al. 24746* (K, NY); Saramacca River, trail to Coppenam River, rear village, Pakka Pakka, 26 Jun. 1944, *B. Maguire 23965* (K, MO, NY, P, US); Inter Coppename fluv. ostium et Coronie oppidum, 15 Dec. 1948, *J. Lanjouw & J.C. Lindeman 1384* (K, NY); In montibus qui dicuntus Nassau, 17 Feb. 1949, *J. Lanjouw & J.C. Lindeman 2146* (K, NY); Jodensavanne-Mapane kreek area, along road to Mapane creek, 21 Dec. 1954, *J.C. Lindeman 6933* (W); Vicinity of Moengo, Cottica River, Adjoema Kondre Hill, trail to Adjoema Kondre Village, 27 Dec. 1954, *R.S. Cowan 39007* (NY, US); Wilhelmina Gebergte, Zuid River, 220 m, 16 Sep. 1963, *H.S. Irwin & al. 55790A* (K, NY, P, US, W) : **2n = 36!** (Gould and Soderstrom 1967); Wilhelmina Gebergte, Kaiser Airstrip, 45 km above confluent with Lucie River, 270 m, 3°20'N,, 26 Sep. 1963, *H.S. Irwin & al. 57618* (K, MO, NY, P, US); Nickerie, area of Kabalebo Dam Project, ca. 20 km SW of Avanavero dam site, 11 Nov. 1976, *N.M. Heyde & J.C. Lindeman 10* (K, MO, NY).

TOBAGO. Belmont woods, 30 Mar. 1910, *W.E. Broadway 3551* (MO); Greenhill, 2 Dec. 1910, *W.E. Broadway 4038* (BM, G, K, L, MO, NY, US); Tobago, centre of the island, 18-21 Dec. 1912, *A.S. Hitchcock 10261, 10262, 10269, 10275* (US); Tobago, 25 Oct. 1925, *W.G. Freeman & L.O. Williams 11426* (K); Parlatuvier-Roxborough Trace, Bloody Bay to road-head above Roxborough, 8 Apr. 1959, *R.S. Cowan 1486* (K, NY, US); Castara Road, 17 Mar. 1963, *L.M. Andrews 610A* (NY); Mount St. George to Hillsborough Dam Road, 5 Jun. 1975, *D. Philcox & A.M. Raynal 7906* (K); Roxborough, 1 Mar. 1981, *C.D. Adams & Y.S. Baksh 323* (MO, NY); St. Paul Parish, NNW of Roxborough, 6 Jan. 1989, *R.D. Worthington 17634* (NY).

TRINIDAD. Tabaquite, 10 Dec. 1912, *A.S. Hitchcock 10170* (L, US); Cedros, 12-14 Dec. 1912, *A.S. Hitchcock 10151* (L, US); Port of Spain, 26 Dec. 1912, *A.S. Hitchcock 9962* (US); St. Joseph, 30 Dec. 1912, *A.S. Hitchcock 10020* (US); Cedros, Dec. 1914, *A.S. Hitchcock 33391* (L); Samana, near the Rest House, 14 Jan. 1915, *W.E. Broadway 4952* (US); Morne Blue, 13 Mar. 1921, *N.L. Britton & al. 2266* (G, K, NY, US); Heights of Aripo, 10-26 Jan. 1922, *W.E. Broadway 9929* (K, NY, US); Morne Blue, 18 Dec. 1924, *W.E. Broadway 5504* (BM, K, MO); Aripo, 15 Jan. 1926, *W.E. Broadway 5892* (BM, K, MO, US); Blanchisseuse road, 10 Nov. 1929, *W.E. Broadway* 7666 (G); Zamsel Hill, Arouca, 15 Feb. 1928, *W.E. Broadway 6811* (BM, K, MO); Rain forest on slopes above Oropuche River (on Valencia-Matura Road), 19 Jun. 1963, *T.R. Soderstrom 1036* (US); About 1 mile outside of Tabaquite, 21 Jun. 1963, *T.R. Soderstrom 1071* (US); Northern Range, 4 miles N of the intersection (along the Heights of Guanapo Road) of the Heights of Guanapo Road and Eastern main road (intersection 1 mile E of Arima), 200 m, 30 Jul. 1970, *G. Davidse 2461* (MO); Peninsula between La Vache and Maracas Bays, mile post 5 along the North Coast Road, 280 m, 5 Aug. 1970, *G. Davidse 2566* (MO); Ca. 2 miles NE of Point Fortin, 20 m, 6 Aug. 1970, *G. Davidse 2579* (MO); Above Spring Hill, Arima-Blanchisseuse road, 26 Dec. 1976, *C.D. Adams 14168* (K); Manzanilla Bay, 22 Nov. 1977, *C.D. Adams 341* (NY); On the Blanchisseuse Road at mile 10 N of Arima, 16 Jan. 1982, *N.A. Harriman 17501* (NY).

VENEZUELA. Amazonas. Raudal Montserrat, 19 Sep. 1951, *L. Croizat 677* (NY); Caño Ceiba, Rio Venturi, 4 Dec. 1975, *Lister 103* (K); Caño Mosquito on Cano Marita, 2 Feb. 1976, *Lister 187* (K); Sta. Elena, Mata Cutia, 11 Nov. 1979, *N.A. Rosa & O.C. Nascimento 3388* (NY); Río Negro, 1.5 km E of Cerro de La Neblina, 140 m, 0°50'N, 66°10'W, 2-3 Dec. 1984, *R. Liesner 17412* (K, MO, US); Vicinity of Neblina base camp along Rio Mawarinuma, 140 m, 0°50'N, 66°10'W, 4 Dec. 1984, *T.B. Croat 56617* (MO, NY, US); Depto. Atures, E slope of a peak, 8 km NW of Yutaje, 4 km W of Rio Coro Coro, W of Serranda de Yutaje, 05°41'N, 66°10'W, 4 Mar. 1987, *R. Liesner & B. Holst 21608* (MO, NY); Depto. Atabapo, Alto Rio Cunucunuma, Poblacion Culebra, 190 m, 03°45'N, 65°45'W, Apr. 1990, *Á. Fernandez 7567* (MO); **Anzoátegui**. Distr. Freites, Burro trail between San Durrial and Los Pajaritos, 30 km by air ENE of Bergantín and N of Mundo Nuevo, 1200-1400 m, 10°03'N, 64°06'W, 1 Dec. 1981, *G. Davidse & A.C. Gonzalez 19775* (MO); **Bolívar**. Alrededores Km 88, carretera El Dorado, Nov. 1958, *L. Aristeguieta 3712* (MO, NY, VEN); Cerro Uroi, Rio Uroi, 13 Sep. 1962, *B. Maguire & al. 53806* (NY); **Cojedes**. Pao, Las Galeras de El Pao, carretera El Tinaco-El Baul, 9°30'N, 68°10'W, Oct. 1988, *M. Ramia 8779* (K, MO); **Guárico**. Estación Biologica de los Llanos, a unos 10 km al SE de Calabozo, 7 Aug. 1989, *F. Zuloaga & M. Ramia 4355* (K); **Isla de Margarida**, Nueva Sparta, Cerro Copey, 11°2'N, 63°55'W, 24 Mar. 1985, *J.A. Steyermark & al. 131009* (MO, NY); **Miranda**. Distr. Paez, Fila de Guayas between Rio Guayas and Rio Guapo, ca. 15 km SW of El Guapo, 400-700 m, 10°04'N, 66°04'W, 6 Jun. 1977, *G. Davidse & A.C. Gonzalez 13648* (MO); Selva Riverina cerca de Puente Galipero comunidad indigena de indios Guahibo a unos 30 km de Puerto Ayacucho, 100 m, 9 Jan. 1978, *J. Bono 8* (FT); Cerro Bachiller, W of Caño Rico, 21 Mar. 1978, *J.A. Steyermark & G. Davidse 116550* (MO, NY); **Sucre**. Distr. Benitez, primary forest on low ground along Caño Ajies, N of Ajies, 10°28'N, 63°05'W, 18 Feb. 1980, *J.A. Steyermark & al. 121318* (MO).

VIRGIN ISLANDS. St. Croix. North slope of Bodkin Hill, 2 Feb. 1974, *F.R. Fosberg 55312* (MO, US); **St. John.** Cruz Bay Quarter, dirt road to Susannaberg, 8 Jan. 1991, *P. Acevedo-Rodriguez & A. Siaca 3844* (NY); **Tortola**. 18-21 Feb. 1913, *J.A. Shafer 1147* (NY, US); Road to Sage Mountain, 23 Feb. 1988, *P. Acevedo-Rodriguez 2681* (NY).

WINDWARD ISLANDS. Martinique. Chemin de St. Pierre, Jan. 1854, *C. Belanger 782* (FI-Webb); Martinique, 1870, *L. Hahn 1158* (G, K); **Guadeloupe**. s.d., *C. Bertero s.n.* (TO); **St. Lucia**. 6 Dec. 1929, *N.Y. Sandwith s.n.* (K).

(8) ***Lasiacis linearis*** Swallen, Phytologia 4: 427. 1953. (Fig. 22).

Type: *Guatemala, Zacapa, Sierra de las Minas, below Finca Alejandria, pine covered canyon bordering Rio Lima, 2000 m, 14 Oct. 1939, J.A. Steyermark 30046* (holotype: F (photo!) [Acc. No. 1044422F]).

Description

Perennials, caespitose. *Culms* 50-75(-100) cm tall, mostly creeping, decumbent, rooting at nodes, branch-

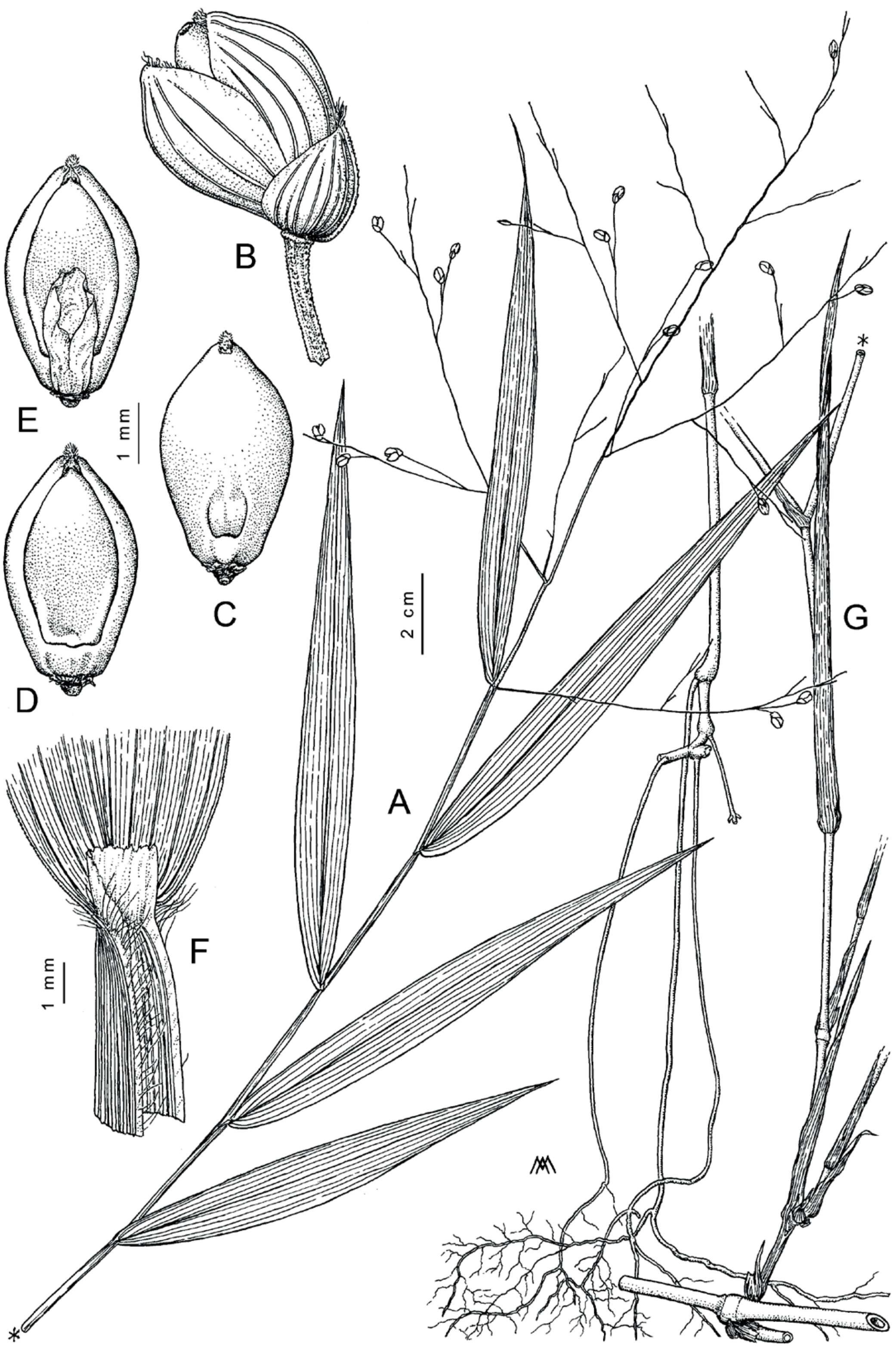

Figure 22. *Lasiacis linearis* Swallen: **A.** Habit; **B**. Spikelet lateral view; **C**. Fertile upper floret dorsal view; **D**. Fertile upper floret ventral view without lower persistent palea; **E**. Fertile upper floret ventral view with lower persistent palea [A-E. from *C.V. Morton 6954* (K)]; **F**. Ligular area; **G**. Culm with persistent leaf sheaths, and basal area rooting at the nodes [F-G. from *G. Davidse & R.W. Pohl 2106* (L)]. *A. Maury delineavit*.

ing, straggling; *internodes* 2–5 mm thick, slender, solid, usually glabrous, upper part puberulent; *nodes* glabrous. *Leaf sheaths* shorter than internodes, puberulent to pubescent, hairs up to 0.8 mm long, overlapping margins ciliate with small hairs up to 0.4–0.5 mm long; *collars* puberulent throughout; *ligules* 1.5–4.0(–4.8) mm long, conspicuous, usually dark brown, apex erose to lacerate, with hairs 1.5–2.8 mm long; *blades* 16–22 cm long, 0.8–1.3 cm wide, base slightly acuminate, apex acuminate to attenuate, adaxial surface glabrous and scabrid, abaxial surface glabrous with margin scabrid. *Panicles* up to 30–35 cm long; *branches* scabrid widely spreading, distally bearing long-pedicelled spikelets. *Spikelets* 4–4.5 mm long, 2.0–2.5 mm wide, narrowly obovate, often purplish at immaturity; *lower glumes* 2.0–2.5 mm long, 2.0 mm wide, 7–10-veined; *upper glumes* 2.8–3.2 mm long, 2.0 mm wide, 8–11-veined; *sterile florets* without a flower, *lemmas* 9–11-veined, *paleas* ½ long the length of the fertile floret; *fertile florets* 4–5 mm long, 2.5–3.0 mm wide, *anthers* 1.5–1.8 mm long, white, *stigmas* purple; *caryopses* 2.2–2.5 mm long, 1.5–1.8 mm wide. *Chromosome number*: *n* = 18 (Davidse 1972, 1978).

Vernacular names

Panama: Chiriquí, "*bambito*" *E.L. Tyson 5666* (MO, US).

Distribution

Belize, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama. (Fig. 23).

Distribution (bibliographic references)

Swallen (1953, 1955b); (Davidse 1978, 1994); Pohl (1980); D'Arcy (1987); Morales (2003); Correa et al. (2004); Sutherland (2008); Dávila et al. (2018); Villaseñor (2016); Sánchez-Ken (2019); Menjívar Cruz et al. (2021).

Figure 23. *Lasiacis linearis* Swallen: general geographic distribution.

Ecology

Cloud forests and oak-pine forests in Central America. Between 1400-2400 m [*J. Menjívar & R.M. Baldini 3616, 3624* (FT, LAGU, MHES) and *E.M. Martinez S. & al. 13218* (MO)].

Phenology

June/July and October through April.

Remarks

Lasiacis linearis presents much affinity to other species from Central America such as *L. oaxacensis*, *L. sloanei*, and *L. standleyi*, with procumbent growth habit, and rooting at the nodes. *Lasiacis linearis* prefers cool, high montane habitats if compared with the adaptability even in low altitude habitats of *L. oaxacensis* and *L. sloanei*, and it is considered a Mesoamerican endemic species with a peculiar distribution and ecology.

Selected specimens

BELIZE. Belize. Belmopan, 5 Mar. 1974, *W.C. Verboom 5075* (K).

COSTA RICA. **Cartago**. Cerro Tabalzo, 20 Aug. 1982, *R.W. Pohl 14135* (K, MO, NY); **Puntarenas**. Cordillera de Talamanca, area between headwaters of Río Bella Vista and Sitio Coton, 2000 m., 9°49'N, 82°46'W, 25 Aug. 1983, *G. Davidse & al. 24055* (MO); Buenos Aires, Parque Nacional de La Amistad, Cuenca Térraba-Sierpe, Buenos Aires, potremo Grande, Tres Colinas, PILA, Herbazal arbolado por *Quercus burnelloides*, *Cornus disciflora, Freziera candidans*, *Quercus insignis* y *Clethra*, 9°08'17"N, 83°04'12"W, 200-2100 m, 28 Feb 2008, *D. Solano 5213* (PMA); **San José**. Z.P. Cerros de Escazú, carretera a Fila El Cedral, 1900 m., 9°50'02"N, 84°06'40"W, 22 Sep. 1993, *J. Morales 1746* (MO).

EL SALVADOR. San Salvador. Volcán San Salvador, El Boquerón, 1650-1800 m, 13°45'50'N, 89°16'15"W, 4 Feb. 1998, *A. Monro & al. 2194* (MO); **Santa Ana**. Parque Nacional Montecristo, Cordillera de Matapán, 89°22'W, 14°27'N, 27 Jan. 1998, *G. Davidse & al. 37167* (BM, MO); Metapán, Parque Nacional Montecristo; Camino a Miramundo, por Puente Oriconte, 1900 m, 3 Sept. 2002, *R.A. Carballo 444* (BM, LAGU, MO); Metapán, Santa Ana, P.N. Montecristo, arriba de la cabaña cientifica, 1900 m, 14°25'N, 89°21'W, 29 May 2002, *J. Monterrosa 222* (MO); Metapán, Santa Ana, Parque Nacional Montecristo, hacia El Trifinio, 14°24'56"N, 89°21'17"W, 2235 m, 11 Feb. 2016. *J. Menjívar & R.M. Baldini 3616, 3624* (FT, LAGU, MHES).

GUATEMALA. El Progresso. Hills between Finca piamente and slopes SE of Finca Piamente, 4 Feb. 1942, *J.A. Steyermark 43405* (US); **Guatemala**. On dry hillside of River Villalobos, 12-23 Jun. 1966, *A. Molina & al. 16075* (US); Guatemala, vicinity of San Andrecillo, 1700 m, 26 Sep. 1972, *A. Molina R. & A.R. Molina 27555* (MO); **Huahuetenango**. Chanximil, Aldea San Martin, Todos Santos Cuchumatan, 2185 m, 16 Sep. 2006, *J. Morales 3895* (MO); **Quiché**. Sierra madre Mountains between Los Encuentros and Chichicastenango, 1800-2000 m, 22-23 Dec. 1972, *L.O. Williams & al. 41632* (MO); **San Marcos**. Near Aldea Fraternidad, between San Rafael Pie de la Cuesta and Palo Gordo, 10-18 Dec. 1963, *L.O. Williams & al. 6097* (NY, US); **Sololá**. Volcán Atitlan, 11 Jun. 1942, *J.A. Steyermark 47347* (US).

HONDURAS. **Lempira**. Cerro Oeste Río Naranjo, bosque nublado latifoliado en el filo a cerro Oeste del Río Naranjo, Parque Nacional de Celaque, 9 Jul. 1991, *P. House 1035* (MO); Parque Nacional Celaque, along trail from old electricity generation plant to Camp Don Tomas, ca. 10 straight line WSW of Gracias, 1850 m, 14°33'N, 88°40'W, 11 Feb. 1993, *R. Evans 1163B* (MO). **Morazán**. Mt. Uyuca, 2000 m, 2 Mar. 1947, *L.O. Williams & A. Molina 12112* (US); Mt. Uyuca, 26 Jun. 1947, *A. Molina 205* (BM, US); Mt. Uyuca, cloud forest, 16 Jun. 1948, *S.F. Glassman 1625* (NY); Mt. San Juancito, 18 Jul. 1948, *S.F. Glassman 1972* (NY); Cerro de Uyuca, trail between Las Flores and La Labranza, 22 Aug. 1949, *P.C. Standley 23126* (NY, US); Cerro de Uyuca, 10-20 Mar. 1951, *C.V. Morton 6954* (K, NY, US); Mt. Uyuca, 19 Oct. 1951, *J.R. Swallen 10900* (MO, US); Morazán, Sierra San Juancito, road to San Juancito, 27-28 Oct. 1951, *J.R. Swallen 11138* (US); La Tigra, Presa La Tigra, 29 Nov. 1958, *J.G. Hawkes 2131* (US); Cloud forest, Mount Uyuca, 1500-1800 m, Aug. 1960, *H.W. Pfeifer 1447* (US); Mountains above San Juancito, 7500 ft, cloud forest, Aug. 1960, *H.E. Pfeifer 1879* (US); Cerro de Uyuca, near Zamorano, 1 Jul. 1962, *G.L. Webster & al. 11898* (US); Cerro Uyuca ca. 8 km W of El Zamorano, 1800 m, 16 Jun. 1970, *G. Davidse & R.W. Pohl 2100* (MO), *2106* (K, L, MO, NY, US), ***n* = 18!** (Davidse 1978); Cerro La Tigre, ca. 11 km NE of Tegucigalpa, 1800 m, 17 Jun. 1970, *G. Davidse & R.W. Pohl 2121* (K, L, MO, NY, US); Montaña de Celaque, SE part of massif, represa trail from Gracias to top of mountain, 2300-2400 m, 14°33'N, 88°40'W, 25 May 1991, *G. Davidse & R. Zuniga 34756* (MO).

MEXICO. **Chiapas**. Sierra Madre, 3 Nov. 1960, *T. Tateoka 1031* (US); Chiapas, Union Juárez, en el volcán Tacaná, entre Talquian y la cima del volcán, 1600-2400 m, 19 Jun. 1985, *E.M. Martinez S. & al. 13218* (MO); Chiapas, San Fernando, carretera San Fernando-Chicoasen, 900 m, 16°54'12"N, 93°08'44"W, 17 Dec. 2007, *J.A. Espinosa Jimenez 534* (MO).

PANAMA. **Chiriquí**. Chiriquí Volcano, Sep. 1911, *A.S. Hitchcock 8201* (US); Valley upper Río Chiriquí, vicinity of Monte Lirio, 27 Jun.-13 Jul. 1935, *R.J. Siebert 278* (MO, NY, US); Ca. 2 miles W of Cerro Punta, clambering near Río Chiriquí Viejo, 1630 m., 17 Jan. 1968, *S. McDaniel 10048* (MO); Bambito, 1 mile SW Cerro Punta, 5600 ft, forest shade, 26 Jun. 1969, *E.L. Tyson 5666* (MO, US); Cerro Punta, in deep shade, 6000 feet., 27 Jun. 1969, *E.L. Tyson 5802* (MO, SCZ); E of Boquete along steep, forested slopes and in wooded pastures on Cerro Azul near Quebrada Jaramillo, 1620-1700 m., 11 Aug. 1974, *T.B. Croat 26858* (MO); E slope of Volcán de Chiriquí (Barú), WNW of Boquete, partially cleared slopes with patches of original oak forest and mostly secondary growth, 1900-2000 m, 19 Nov. 1975, *G. Davidse & W.G. D'Arcy 10162* (MO, US); W end of high ridge N of Barú summit, 8 Apr. 1979, *B. Hammel & al. 6941* (MO); Near Fortuna Dam Camp, beside gravel road, 08°43'N, 82°14'W, 25 Feb. 1985, *R.J. Hampshire & C. Whitefoord 59* (PMA); Along road to top of Volcano Barú, 1800 m, 08°45'N, 82°30'W, 1800 m, 28 Jul. 1987, *G. McPherson 11332* (MO, PMA); Renacimiento, Jurutungo, carretera de acceso a la Finca Los Quetzales, 1870-1935 m, 8°54'N, 82°44'W, 27 Sep. 1996, *C. Galdames 3459* (MO, NY, PMA, SCZ).

(9) *Lasiacis maculata* (Aubl.) Urb., Symb. Antil. 8: 751. 1921. (Fig. 24, 25, 26).

Bas.: *Panicum maculatum* Aubl., Fl. Guiana Fr. 1: 51. 1775.

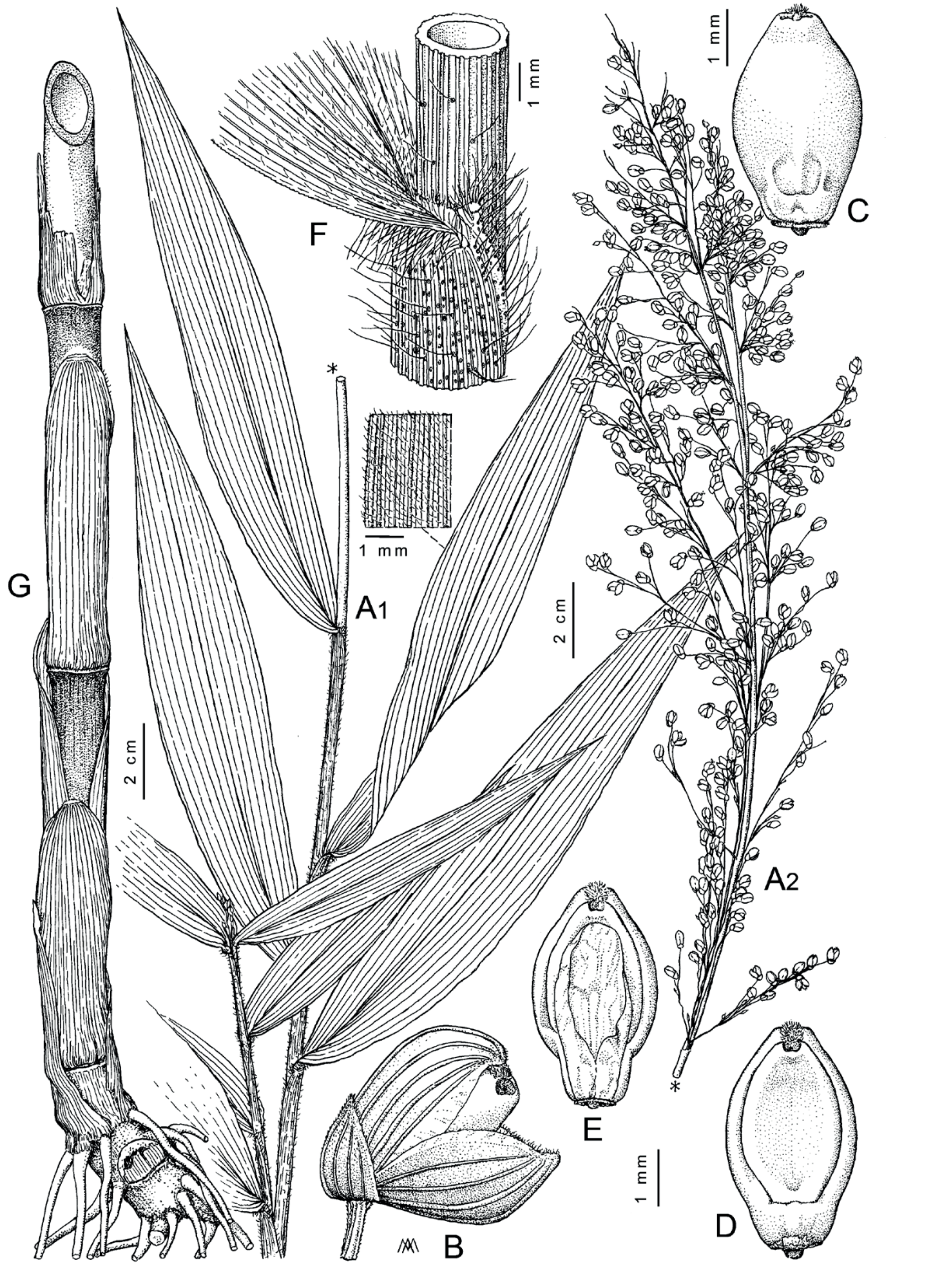

Figure 24. *Lasiacis maculata* (Aubl.) Urb.: **A1**. Habit; **A2**. Apical part of the culm with fertile branches; **B**. Spikelet lateral view; **C**. Fertile upper floret dorsal view; **D**. Fertile upper floret ventral view without lower persistent palea; **E**. Fertile upper floret ventral view with lower persistent palea [B-E. from *A.F. Skutch 3817* (K)]; **F**. Ligular area; [A1, A2 & F. from *A. Ratter & al. 2120* (K)]; **G**. Lower robust culm with persistent leaf sheaths, and prop roots at the base. [G. from *R.M. Harley & R. Souza 11074* (K)]. *A. Maury delineavit.*

Figure 25. *Lasiacis maculata* (Aubl.) Urb.: dense inflorescence (Panama, Veraguas, photo R.M. Baldini).

Figure 26. *Lasiacis maculata* (Aubl.) Urb.: general erect to procumbent habit (Panama, Veraguas, photo R.M. Baldini).

Type: Plumier MS 4: ic. 82. (holotype: P! Bibliothéque Central du Museum National d'Histoire Naturelle). *Martinique environs de St. Pierre, Mai 1853*, *Belanger 390*" (epitype: FI! [barcode FI012314]; isoepitypes G! [barcode G00614203], P! Two sheets [barcode P00633954, P01931995] (see also Baldini, 2010: 114)).

(=) *Panicum lanatum* Sw., Prodr. Veg. Ind. Occ. 24. 1788, *nom. illeg.*, non Rottb. (1776).

Type: "*Jamaica, Swartz s.n.*". (**lectotype, designated here**: S (photo!) [Acc. No. S-R-3976]; isolectotypes: S (photo!) [Acc. No. S-R-3974], BM! [barcode BM000938727], US! Fragment from S [barcode US00148223]).

(≡) *Panicum divaricatum* L. var. *lanatum* (Sw.) Kuntze, Rev. Gen. Pl. 2: 784. 1891.

(=) *Panicum sorghoideum* Ham ., Prodr. Pl. Ind. Occ. 10. 1825.

Type: "*Porto Rico, Desvaux Herb. No. 24*". (holotype: P! [barcode P00633952]; isotype US! Fragment from P [barcode US00140003]).

(≡) *Panicum lanatum* Sw. var. *sorghoideum* (Ham.) Griseb., Fl. Brit. W. Ind. 551. 1864.

(≡) *Lasiacis sorghoidea* (Ham.) Hitchc. & Chase, Contr. U.S. Natl. Herb. 18: 338. 1917.

(=) *Panicum divaricatum* L. var. *latifolium* Schlecht. & Cham., Linnaea 6: 33. 1831, non E.Fourn. (1886).

Type: Nova Hollandia?, "*Sieber 120*" (lectotype designated by Baldini (2010: 116): HAL! [barcode HAL0106587]; isolectotypes: G! Three sheets [barcode G00176060, G00176061, G00176062]; L! [barcode L0797238], PI! [Acc. No. 0411253], W! [barcode W0005812]).

(=) *Panicum praegnans* Steud., Syn. Pl. Glum. 1: 74. 1854.

Type: "*Mexico, Oaxaca, Buchinger 488*." (lectotype, designated by Hitchcock (1920: 26): P! [barcode P00633953]; isolectotype: US! Fragment from P [barcode US00139891]).

(≡) *Panicum maculatum* Aubl. var. *pilosum* E.Fourn., Mex. Pl. 32. 1886. Based on *P. praegnans* Steud . (1854).

(=) *Panicum martinicense* Griseb., Fl. Brit. W. Ind. 552. 1864.

Type: "*Martinique*, *Flora martin. Nro. 29, Sieber 1822*" (lectotype, designated by Davidse (1978): GOET! [barcode GOET006592]; isolectotypes: L! Two sheets [barcode L0797212, L0797213], MO! [Acc. No. MO126663], US! Two sheets [barcode US00132971, US00132972], W! Two sheets [Acc. No. W0005811, W1889021140]).

(=) *Panicum guaraniticum* Speg., Anales Soc. Ci. Argent. 16: 107. 1883.

Type: "*Panicum guaraniticum Sp. (*n.sp.*), Misiones, Posadas, Mar. 1883, von Gülich s.n.*" **lectotype, designated here**: LP! (photo) [barcode LP001599]; syntypes: LP! (photo), four sheets [barcode LP001600, LP001601, LP001602, LP001603], BAA! (photo) [barcode BAA00000408].

(≡) *Lasiacis guaranitica* (Speg.) Parodi, Notas Mus. La Plata, Bot. 8: 95. 1911.

(=) *Panicum swartzianum* Hitchc., Contr. U.S. Natl. Herb. 12: 140. 1908, *nom illeg. hom*. Based on *Panicum lanatum* Swartz (1788).

(≡) *Lasiacis swartziana* (Hitchc.) Hitchc., Bot. Gaz. (Crawfordsville) 51: 302. 1911.

(=) *Lasiacis patentiflora* Hitchc. & Chase, Contr. U.S. Natl. Herb. 18: 338. 1917.

Type: "*Tobago, center of island, edge of woods on mountainside, 20 December 1912, A.S. Hitchcock 10268*" (holotype US! [barcode US00134119]; isotypes, US! [barcode US00134118], L! Two sheets [barcode L0797276, L0797277], W! [Acc. No. W19280008751]).

(≡) *Lasiacis sorghoidea* (Ham.) Hitchc. & Chase var. *patentiflora* (Hitchc. & Chase) Davidse, Ann. Missouri Bot. Gard. 64: 375. 1977.

(≡) *Lasiacis maculata* (Aubl.) Urb. var. *patentiflora* (Hitchc. & Chase) Baldini, **comb. nov. & syn. nov.**

(-) *Panicum orinocense* Willd. ex Spreng., Syst. Veg. 1: 316. 1825, *nom. inval.,* as *syn*. of *Panicum glutinosum* Lam. (1791). The lectotypification of Baldini (2010): 116 is ineffective as this is an invalid name.

(-) *Panicum arborescens* Sieb. ex Trin., Gram. Pan. 208. 1826, *nom. inval.* as *syn.* of *Panicum latifolium* L. (1753). The lectotypification of Baldini (2010: 116) is ineffective as this is an invalid name.

(-) *Panicum fuscum* Sieb. ex C.Presl, Abh. Böhm. Ges. Wiss. 3: 550. 1845, non Sw. (1788), *nom. inval.* as *syn.* of *P. glutinosum Sw.*(1788). The lectotypification of Hitchcock 1920: 26 is ineffective as this is an invalid name (see also Baldini (2010): 116).

(-) *Panicum glutinosum* J.Presl ex Griseb., Fl. Brit. W. Ind. 552. 1864, non Sw. (1788) nec Lam. (1791), *nom. inval*., as *syn*. of *Panicum martinicense* Griseb. (1864).

Description

Perennials, robust caespitose. *Culms* 1-10 m tall, erect at the base, strongly vigorous, arching and leaning on nearby vegetation; *internodes* 5-15(-18) mm thick, strongly lignified, glabrous to papillose-pubescent; *nodes* glabrous. *Leaf sheaths* papillose-pubescent especially toward the apex, hairs 1.5-4.0 mm long, overlapping margin and throat ciliate; *auricules* with hairs 2.5-3.8 mm long; *collars* hispid and pilose; *ligules* 0.3-1.5 mm long, inconspicuous usually ciliate with hairs 0.5-1.5 mm long; *blades* 5.0-24 cm long, 1.2-4.5 cm wide, very variable from elliptic-lanceolate to lanceolate or linear-lanceolate, acuminate, base asymmetrical and ciliate, adaxial surface puberulent, abaxial surface velutinous to puberulent, margin scabrid. *Panicles* 5.0-25(-35) cm long; *branches* ascending, largely spreading at maturity, scabrous to pubescent. *Spikelets* 3.5-4.5 mm long obovate to elliptic, purple when immature; *lower glumes* 1.2-2.5 mm long, 7-11-veined; *upper glumes* 3.2-4 mm long, 9-13-veined; *sterile florets* sometimes staminate, *lemmas* 9-11-veined, *paleas* 2/3 to equal to the length of the fertile floret; *fertile florets* 3.0-4.0(-4.3) mm long, 2.5-3.0 mm wide, dark brown, clearly indented on the dorsal surface of the lemma, *anthers* 2-2.5 mm long, whitish, *stigmas* white; *caryopses* 1.8-2.3 mm long, 1.5-1.7 mm wide. *Chromosome number*: $n = 9$ (Gould and Soderstrom 1970); $n = 18$, $2n = 36$ (Davidse 1972, 1978); $2n = 36$ (Killeen 1990).

Iconographs

Lámina 148 E as *L. sorghoidea* (Desv.) Hitchc. & Chase (Steyermark and Huber 1978); Fig. 40 C-D as *L. sorghoidea* (Desv.) Hitchc. & Chase (Renvoize 1984); Fig. 183 A-D as *L. sorghoidea* (Desv.) Hitchc. & Chase (Acevedo-Rodríguez 2005); Lámina 156 (Catasús Guerra 2012b); Morrone & Zuloaga as *L. sorghoidea* (Desv.) Hitchc. & Chase (2012: 334).

Vernacular names

Argentina: Misiones, "*tacuapi*" *Montes 2198* (K, US), "*picauilla*" *Montes 2232* (Davidse 1978); **Belize**: El Cayo, "*rat rice*" *P.H. Gentle 2196* (K, NY, US); Stann Creek "*wild rice*" *P.H. Gentle 1910* (K, NY, US); **Bolivia**: Santa Cruz, "*tacuarilla*" *M. Saldias & al. 5029* (MO), "*taquarilla*" Killeen (1990); **Brazil**: Paraná, "*taquaril*" *J.M. Pires & P.B. Cavalcante 52138* (K, MO, NY, US); "*canna de passarinho*" (Quattrocchi 2006); **Colombia**: Meta, "*carrizo*" *X. Londoño & I. D. Quintero 283* (US), "*cola de caballo*" (Quattrocchi 2006); **Costa Rica**: San José, "*cañuela*" *Jiménez 3717* (Davidse 1978); **Dominican Republic**: "*carrizo*" (Acevedo-Rodríguez and Strong 2012); **Ecuador**: Los Ríos, "*carrizo*" *M. Acosta Solis 10696 (*US); Guyas, "*tundilla*" *M. Acosta Solís 5216* (US); Pichincha, "*nankuchip*" *K.S. Lowell 488* (NY); Tungurahua, "*carrecillo*" *M. Acosta*

Solis 10263 (US); **Mexico**: Oaxaca, "*con yana*', *yaga bii*, *guichi yaa*, *xhaga la*, *copachil*, *bara seda xiñá*, *guie' se*', *yaga xuga*, *guichi bihui*, *sabi guini*, *guie' niza*, *chumaga*" *F. Sánchez L. 170* (US); **Paraguay**: Santa Cruz, "*tacuarilla*" *F. Mereles & L. Ramella 2717* & *2804* (G), "*takua vovō*", "*takuaní*", "*takuapi*", "*takuapi guasu*", "*tacuarita*" (Morrone and Zuloaga 1994); **Perú**: Amazonas, "*nagkuship*" *E. Ancuash 562* (US); Maynas, "*carrocillo*" *M. Rimachi Y. 1148* (US); Pasco, "*caricillo morado*" *J. Salick 7319* (MO, NY); San Martín, "*caricillo*" *J. Schunke Vigo 6138* (MO, NY); San Martin, "*carrizo*", "*huaymantillo*", *J. Schunke Vigo 8241* (MO, NY); **Suriname**: Sipaliwini river, "*síkiman ruwe*" (Boejharat 2015); "*nángkuchip*" (Quattrocchi 2006).

Ethnobotanical and economic uses

Bolivia: Santa Cruz, "*very palatable, a source of forage in the dry season*" (Killeen (1990); **Colombia**: Meta, "*mold for molten lead*" *X. Londoño & I. D. Quintero 283* (US); **Ecuador**: "*cattle and guinea pig feed*" (Bennet 1990); **Suriname**: Sipaliwini River "*flutes and pan pipes*" (Boejharat 2015).

Distribution

Argentina, Belize, Bolivia, Brazil, Colombia, Costa Rica, Cuba, Dominican Republic, Ecuador, El Salvador, French Guiana, Guatemala, Guyana, Haiti, Honduras, Jamaica, Leeward Islands, Mexico, Nicaragua, Panama, Paraguay, Perú, Puerto Rico, Suriname, Trinidad & Tobago, USA (Louisiana), Venezuela, Virgin Islands, Windward Islands. (Fig. 27).

Distribution (bibliographic references)

Hitchcock (1909) as *Panicum swartianum* Hitchc.; Hitchcock (1911, 1913) as *L. swartiana* (Hitchc.) Hitchc.; Hitchcock and Chase (1917); Hitchcock (1920, 1922, 1927a, 1930, 1936); Urban (1921: 32); Standley

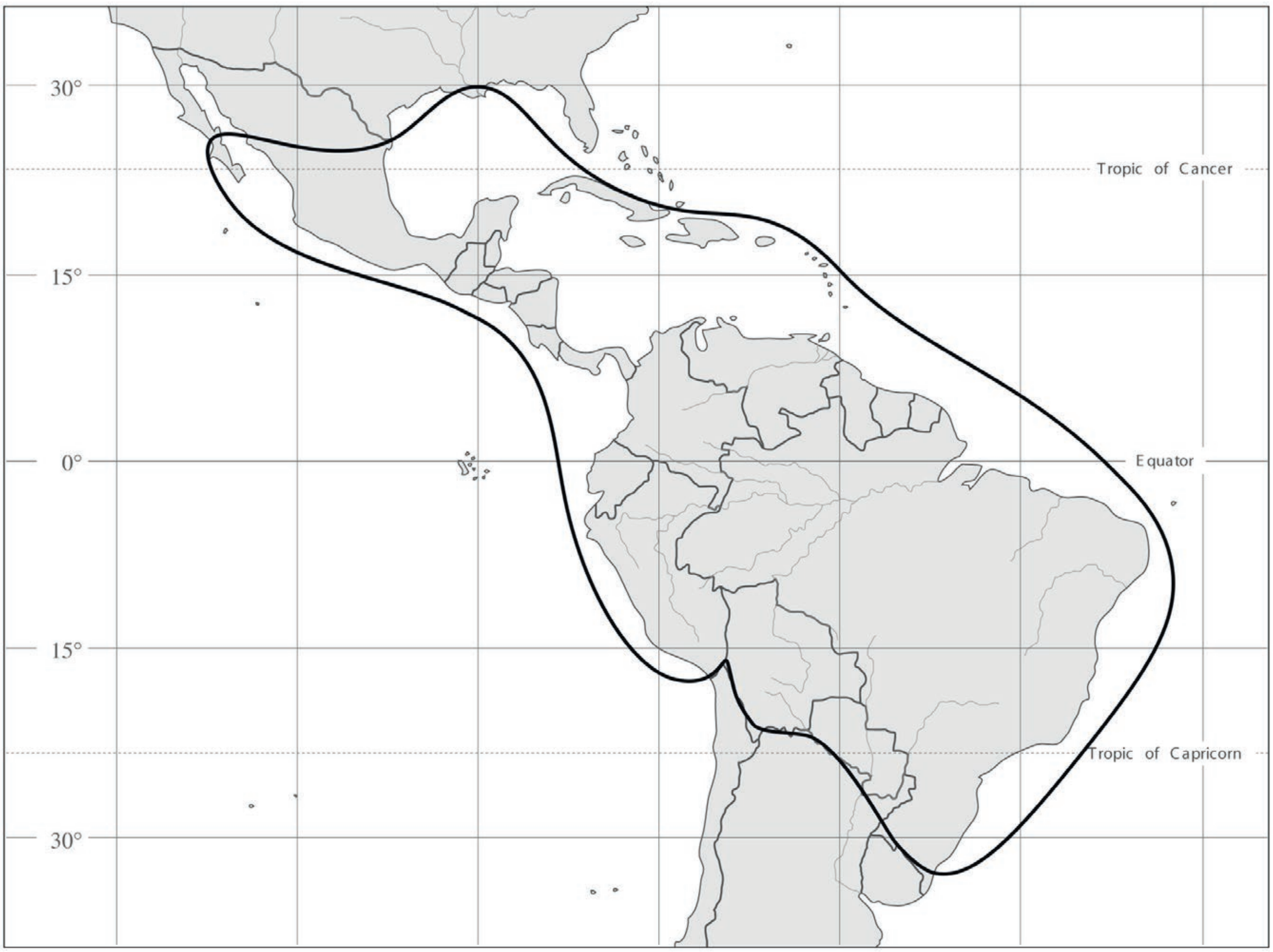

Figure 27. *Lasiacis maculata* (Aubl.) Urb.: general geographic distribution.

and Calderón (1925); Standley (1937); Amshoff and Henrard (1948); Swallen (1931, 1936, 1943, 1955b); Lemée (1955); Foster (1966); Pinto-Escobar (1966); Croat (1978); Beetle (1977); Steyermark and Huber (1978); Howard (1979); Pohl (1980); Smith et al. (1982); Hoyos (1985); Killeen (1990); D'Arcy (1987); Bono (1996); Cialdella and Vega (1996); Judziewicz (1990); Zuloaga and Morrone (1994); Morrone and Zuloaga (1994); Davidse (1978, 1994, 2001, 2004); Rogers and Holder (1999); Serna and Lopez-Ferrari (2000); Zuloaga et al. (2003); Renvoize (1984, 1998); Santos and Sano (2001); Morales (2003); Bussmann (2003); Correa et al. (2004); Acevedo-Rodríguez (2005); Ibáñez et al. (2005); Renvoize et al. (2006); Davidse et al. (2007); Sutherland (2008); Hokche et al. (2008); Morrone et al. (2008); Bono (2010); Giraldo-Cañas (2011); Morrone and Zuloaga (2012); Acevedo-Rodríguez and Strong (2012); Boejharat (2015); Villaseñor (2016); Sylvester (2017); Dávila et al. (2018); Furuya et al. (2019); Sánchez-Ken (2019), all as *L. sorghoidea* (Ham.) Hitchc. & Chase. or related synonyms.

Urban (1921: 751); Adams (1972); Baldini (2010), Catasús-Guerra (2012a) and Menjivar et al. (2012) use the correct applied name *L. maculata* (Aubl.) Urb., while Villavicencio et al. (2014) report erroneously this species either as *L. sorghoidea* or as *L. maculata*.

Ecology

Various types of habitats, predominantly along secondary forest edges, roadsides, edges of open areas into the forests, including xerophytic habitats at sea level (Mexico: Baja California, *A. Carter & L. Kellogg 3110* (K, US), and edges of savannas. Mostly collected below 1000 m; in southern America up to 2550 m above sea level [Perú: Amazonas, *C. Diaz & al. 3508* (MO)].

Phenology

October through May/June.

Remarks

L. maculata is certainly the species with the widest distribution in the genus with a high vegetative polymorphism regarding pubescence of leaf surface and the culm that would suggest describing many varieties or forms. *Lasiacis maculata* is typically a forest edge species and often acts as a pioneer species in secondary forest restoration as well as *L. ligulata* and *L. ruscifolia*. As in *L. procerrima* [see *Stapf et al. 791* (FT, PMA, SCZ)], *L. maculata* bears solid prop roots at the base of the culm [see *Stapf et al. 828* (FT, SCZ)]. The validity of the name *Lasiacis maculata* is discussed in Baldini (2010).

Selected Specimens

ARGENTINA. **Corrientes**. General Paz, Ita Ibate, 11 Jan. 1946, *T. Ibarrola 4054* (FI); Mburucuyá, Estancia Santa Teresa, 9 May 1952, *T.M. Pedersen 1717* (BR, C, G, NY, P, US); San Cosme, 20 Jun. 1973, *A. Krapovickas & C.L. Cristobal 23624* (G, P); Capital, El Perichón, 1 Mar. 1976, C. *Quarín 3388* (G, K, MO); Berón de Astrada, 15 Jan. 1977, *A. Schinini 14045* (K); Formosa, Piranè, S de Piranè, 13 Jan. 1980, *G. Guaglianone & al. 675* (K, US); Ituzaingó, 12 Apr. 1985, *F.O. Zuloaga 2287* (K); Ituzaingó, Santa Rita, 3 Mar. 1987, *A. Krapovickas & al. 41058* (K); **Formosa**. Pilcomayo, N de Puesto Porteño, 14 Apr. 1947, *I. Morel 2505* (K); Pilcomayo, Formosa, La Laguna Blanca, 13 Mar. 1948, *I. Morel 5041* (W); Formosa, Pilcomayo, Costa Alegre, N de La Primavera, 27 Jan. 1949, *I. Morel 7088* (US); Formosa, Estancia El Ombu, 26°6'6"S, 58°48'6"W, 19 Dec. 2004, *H. Maturo & D. Prado 282* (BM); **Jujuy**. Ledesma, camino al Arroyo Aguas Negras, 24 Feb. 1985, *R. Kiesling 5644* (MO); Ledesma, Ruta Prov. 31, 2 km del desvio de la Ruta Prov. 1, camino a Vinalito, 540 m, 23°43'S, 64°30'W, 21 Feb. 1998, *O. Morrone & al. 2882* (MO); **Misiones**. Posada Loreto, 30 Jan. 1908, *E.L. Ekman 619* (G); Puerto Aguirre, 26 Jan. 1922, *L.R. Parodi 4410* (US); La Grana, 31 Jan. 1922, *L.R. Parodi 4452* (L); S. Ignacio, Puerto Viejo, 21 Mar. 1946, *G.J. Schwarz 2290* (FI); Candelaria, Carpì, 21 Jan. 1946, *B.S. Bertoni 2672* (W); La Mina-St. Juan, 26 Apr. 1946, *J.E. Montes 2198* (K, US); Candelaria, San Juan, 6 Jun. 1947, *E. Schwindt 297* (US); Candelaria, Santa Ana, 15 Jan. 1947, *E. Schwindt 42* (FI); Candelaria, Santa Ana, 11 Nov. 1947, *E. Schwindt 119* (BR, L); San Pedro, Caraguatay, 25 Apr. 1949, *J.E. Montes 1592* (US); San Ignacio, Parque Provincial Teyucuaré, 16°S, 55°33'W, 21 Apr. 1994, *F.O. Zuloaga & al. 5689* (NY); Iguazú, Sendero Macuco, 28 Mar. 1995, *R. Vanni & al. 3305* (K, MO); San Pedro, Parque Provincial Moconá, 230 m, 27°09'S, 53°53'W, 13 Apr. 1996, *O. Morrone & al. 5455* (MO, NY); Iguazú, Parque Provincial Uruguaí, 25°55'S, 54°15'W, 22 Apr. 1997, *O. Morrone & al. 1989* (MO, NY); **Salta**. Oran, Ruta 18, a 3-4 km del Puente Internacional Argentina-Bolivia, 400 m, 22°43'S, 64°43'W, 1 May 2003, *O. Morrone & al. 4530* (MO); **Santa Cruz**. Velasco, 63 km S de San Rafael, camino a San José, Serrania del Diablo, 17°11'33"S, 60°36'21"W, 327 m, 4 Apr. 2006, *M. Dematteis & al. 2228* (G).

BELIZE. Cayo. Cayo, 20 Apr. 1931, *H.H. Bartlett 12954* (NY, US); Vaca, 23 Feb. 1938, *P.H. Gentle 2196* (K, NY, US); **Stann Creek**. Stan Creek-Mullins River Road, 21 Jan. 1937, *P.H. Gentle 1910* (K, NY, US); Stann Creek Distr., near Hope Creek, 9 Feb. 1953, *P.H. Gentle 7873* (G, NY, US); Stann Creek, Sapon Road, 5 Feb. 1954, *P.H. Gentle 8118* (BM, G, NY, US); **Toledo**. Punta Gorda, 9 Jan. 1950, *P.H. Gentle 6945* (BM, C, G, NY, US); Toledo, Union Camp, mixed hardwood forest on trail from Union Camp toward Little Quartz Ridge, 700-730 m, 16°23'53"N, 89°08'37"W, 10 Feb. 1997, *T. Hawkins 1334* (MO).

BOLIVIA. **Beni**. Moxos, San Ignacio de Moxo, 65°35'W, 14°55'S, 12 Apr. 1979, *A. Krapovickas & A. Schinini 34930* (K, US); Ballivián, Espiritu en la zona de influencia del Río Yacuma, 200 m, 29 Sep. 1979, *S. Beck 2590* (K, US); San Borja 75 km hacia La Paz, 950 m, 12 Aug. 1981, *S. Beck 6985* (K, US); Vaca Diez 7.7 km from the road between Riberalta and Guayaramerin, ca. 230 m, 11°05'S, 65°50'W, 17 Sep. 1981, *J.C. Solomon 6297* (MO, NY); Ballivián, Rurrenabaque, 10 Jul. 1991, *S. Beck 18633* (K); Santa Cruz, Guarayos, 6.6 km W of Yotaù, 250 m, 16°12'S, 63°04'W, 12 Jul. 1991, *M. Nee & G. Coimbra 41680* (MO, NY); Ballivián, vicinity of Rurrenabaque, 350 m, 15°33'N, 67°33'W, 18 Aug. 2000, *T.B. Croat & al. 84613* (MO); **Chuquisaca**. H. Siles, hillside right of and entering from the Toma de Agua del Río Limon, Monteagudo, 1375 m, 19°48'S, 63°57'W, 24 Jan. 2001, *K. Wendelberger 398* (MO); Chuquisaca, Prov. Sud Cinti, camino de herradura de Río Nuevo-Altos del Rosal, en direción a la Comunidad de Las Abras, 1800 m, 2053'S, 6415'W, 5 May 2005, *R. Lozano 1275* (MO); **Cochabamba**. 1891, *M. Bang 1289* (G, MO, NY, US, W), *1291* (US); Antahuacano, Nordyungas, Polo-Polo bei Coroico, Oct. -Nov. 1912, *O. Buchtien 3635* (MO, NY, US, W); Espiritu Santo, Jun. 1909, *O. Buchtien 161* (F, G, GH, MO, NY); **La Paz**. Guanai, 2000 ft, May 1886, *H.H. Rusby 191* (US); Sur-Yungas, edge of forest Chulumani, 1600 m, 22 Dec. 1923, *A.S. Hitchcock 22652* (US); Mapiri, San Carlos, 5 May 1927, *O. Buchtien 89* (MO, NY); La Paz, Sud Yungas, Puerto Linares, 13 Jul. 1979, *S. Beck 1668* (K); Nor Yungas, Coroico, 15 Feb. 1980, *T. Feuerer 855a* (K); Sud Yungas, Chulmani, 1700 m, 4 Jul. 1981, *S. Beck 4727* (K, US); Nor Yungas, 950 m, 2 Jan. 1983, *S. Beck 9177* (K, MO, US); Nor Yungas, Caranavi to Coroico, 1050 m, 10 Mar. 1987, *S.A. Renvoize 4744* (K, MO, NY); Nor Yungas, Valle del Río Unduavi, entre Santa Rosa y Machacamarca, arriba de Lamina San Silvestre, 1400 m, 4 Feb. 1988, *R. Seidel & E. Richter 1185* (US); Inquisivi, on the slopes of both sides of the Río Suri between Puente Alegre and the mouth of the Río Khori Camaña, ca. 12 km NE from Licoma Pampa, 1500 m, 16°42'S, 67°10'W, 16 Jun. 1988, *M. Lewis 88843* (MO); Alto Madidí, 360 m, 13°35'S, 68°46'W, 28 May 1990, *A. Gentry & S. Estensoro 70736* (MO); Sud Yungas, Alto Beni, 7 Jul. 1995, *R. Seidel & A. Carrizales 7813* (K, MO); Nor Yungas, ca. 7 km from Coroico on road to Coricata, 25 Jul. 1996, *J.R. Wood 11301* (K); Muñecas, antes de Marumpampa, subiendo ladera con pendiente fuerte al lado de arroyo, 1300 m, 15°13'22"S, 68°40'29"W, 20 Apr. 2005, *A. Fuentes & al. 7041* (MO); **Santa Cruz**. Sará, Buena Vista, 450 m, 15 May 1925, *J. Steinbach 7111* (BM, G, K, MO, NY, US); E of Puerto Suarez, near Brazilian frontier, 5 Mar. 1930, *A. Chase 11154* (US); Ñuflo de Chavez, Concepción, 30 Apr. 1977, *A. Krapovickas & A. Schinini 32064* (K); Sara, Buenavista junto al río Surutú, 8 May 1981, *M. Vazquez Avila 390* (US); Velasco, ca. 122 km N of San Ignacio, 320 m, 15°30'S, 60°57'W, 26 Jul. 1983, *M.J.G. Hopkins & al. #79* (K, MO); Ñuflo de Chavez, E Las Madres, 15 km N of Concepción, 500 m, 16°02'S, 62°00'W, 20 Feb. 1985, *T. Killeen 883* (MO, NY); Ichilo, Parque Nacional Amboró, 700 m, 17°44'S, 63°40'W, 28 Aug. 1985, *J.C. Solomon & S. Urcullo 14088* (K, MO); Ñuflo de Chavez, San Josecito, 2 km NW of Concepción, 500 m, 16°03'S, 62°05'W, 31 May 1986, *T. Killeen 2099* (MO, NY, US, W); Santiesteban, 1.5 km SW of center of Montero, 295 m, 17°21'S, 63°16'W, 12 Jan. 1987, *M. Nee 33436* (K, MO, NY); Andrei Ibanez, along Río Pirai, 495 m, 17°59'S, 63°23'W, 17 Jan. 1987, *M. Nee 33617* (K, MO, NY); Ñuflo de Chavez, Rancho Puesto Nuevo, 40 km S of Concepción, 700 m, 16°25'S, 62°00'W, 26 Feb. 1987, *T. Killeen 2332* (US), **2n = 36!** (Killeen 1990); Cerro San Miguel, 5 Mar. 1989, *L. Ramella & F. Mereles LR2501* (G); Ñuflo de Chavez, Perseverancia, vecindad del Río Negro, tributario del Río Baures, a 75 km S del límite del Depto. de Beni y 150 km W del Río Paragua, 200 m, 14°38'S, 62°37'W, 17 May 1991, *B. Mostacedo 105* (F, MO); Ichilo, 2 km ESE of Santa Fé, 295 m, 17°24'S, 63°49'W, 26 May 1991, *M. Nee 40568* (K, MO, NY); Guarayos, Río San Martin, 15°03'21"S, 61°48'12"W, 8-9 Sep. 1993, *I.G. Vargas 2768* (NY); Velasco, Reserva Forestal, Bajo Paraguá, Laja Granitica, 250-500 m, 14°32'20"S, 61°30'00"W, 12 May 1994, *T. Killien & J. Wellens 6308* (MO); Santa Cruz, Ñuflo de Chavez, ca 25 km N of Estación Tres Cruces, 107 km E of Santa Cruz on railroad, 17°22'S, 62°13'W, 17 Mar. 1995, *J.R. Abbott 16440* (FTG); Angel Sandoval, 3 km al S de la Comunidad San Fernando, 108 m, 17°16'37"S, 58°37'48"W, 2 May 1997, *M. Saldias & al. 5029* (MO); Warnes, 4.3 km S of Highway from Puerto Nuevo to Colonia Okinawa, 17°14'S, 62°49'W, 11 Jan. 1998, *M. Nee 47905* (NY); Cordillera, along road to San Joaquín, 1.3 km E of turnoff at La Mora from Highway from Santa Cruz to Abapó, 500 m, 18°27'30"S, 63°12'W, 14 Mar. 1998, *M. Nee 48671* (G, MO, NY, US); Andrés Ibáñez, along new Highway from Santa Cruz to Abapó, 9 km S of Río Peji bridge, 500 m, 18°03'S, 63°12'W, 2 May 1998, *M. Nee 49200* (MO, NY); Ichilo, Nacional Ambirò, Campamento Mataracú, 375 m, 17°33'S, 63°52'W, 2 Jun. 1998, *M. Nee 49591* (MO, NY); Ñuflo de Chaves, 6-8 km de Concepcion, camino a S.A. Lomerio, 478 m, 16°09'56"S, 62°01'20"W, 28 Mar. 2004, *O. Morrone & M.J. Belgrano 4973* (MO); Ibáñez, 10 km by gravel road SE of San José and the turnoff from Santa Cruz-Samaipata Highway, 17°59'35"S, 63°17'37"W, 3 Apr. 2007, *M. Nee 54974* (NY).

BRAZIL. **Alagoas**. Murici, Fazenda Boa Vista, 9°14'10"S, 35°50'10"W, 3 Aug. 2002, *M.R. Barbosa & al. 2531* (NY); **Amapá**. 13 Jul. 1962, *J.M. Pires & P.B. Cavalcante 52138* (K, MO, NY, US); **Amazonas**. Tabatinga, 27 Nov. 1945, *J.M. Pires & G.A. Black 852* (US); **Bahia**. Valley of the Rio das Ondas, ca. 4 km of Barreiras, road to Santa Rita da Cassia, 550 m, 5 Mar. 1971, *H.S. Irwin & al. 31599* (C, K, MO, NY); Islets and banks of the Rio Corrente, Correntina, 44°38'W, 13°20'S, 26 Apr. 1980, *R.M. Harley 21784* (CEPEC, K, NY, US); Bahia, BR-101, próximo a Texeira de Freitas, 13 Apr. 1992, *G. Hatschbach 57047* (CEPEC); Prado, road from Itamaraju to Cumuruxatiba, 17°08'S, 39°25'W, 20 Oct. 1993, *W. Thomas & al. 10027* (CEPEC, NY); Ilhéus, 3 km N of Rodoviaria, Mata da Esperança, 14°46'55"S, 39°04'09"W, 27 Sep. 1994, *W.W. Thomas & al. 10636* (NY); 5.3 km from Almadina on road to Ibatupa, 14°44'11"S, 39°41'57"W, 4 Apr. 1997, *W.W. Thomas & al. 11423 b* (NY); Oliveira dos Brejinhos, ca. 1,5 km da sede do Município, 16 Apr. 1999, *S. Sant'Ana & al. 775* (CEPEC, NY); Encruzilhada, Rodovia Encruzilhada/Riberão do Lardo, 15°30'54"S, 40°48'51"W, 17 Aug. 2001, *A.M. de Carvalho 6973* (CEPEC, NY); **Ceará**. Crato, 16 Apr. 1934, *J.R. Swallen 4354* (US); Crato, Rodovia Crato-Exu, subida da Chapada do Araripe, 24 Jun. 1987, *Coradin & al. 7787* (K); **Districto Federal**. Ca. 30 km S of Brasilia on road to Belo Horizonte, 700-1000 m, 26 Aug. 1964, *H.S. Irwin & T.R. Soderstrom 5624* (G, P, US, W); Districto Federal, Parque Nacional de Gama, 5 Mar. 1965, *W.D. Clayton 4977* (K, NY); Districto Federal, 3 km S of Sobradinho, 1000 m, 1 May 1966, *H.S. Irwin & al. 15453* (US); **Espírito Santo**. Serra do Caiapó, cerrado island on slope, ca. 38 km S of Caiaponia on road to Jataí, 800-100 m, 17°12'S, 51°47'W, 18 Oct. 1964, *H.S. Irwin & T.R. Soderstrom 7030* (G, K, MO, P, US); **Goiás**. Villa de Amayas, s.d., *G. Gardner 4052* (BM, FI-Webb, P, US); Natividade, Jan. 1840, *G. Gardner 3573* (BM, K, US); Serra Dourada, 30 Jul. 1952, *A. Macedo 3734* (US); Araguaina, at Rio das Lontras, 300 m, 14 Mar. 1968, *H.S. Irwin & al. 21180* (MO, NY, US); 2 km by road W of Monte Alegre de Goiás, 700 m, 13 Mar. 1973, *W.R. Anderson 6950* (K, MO, NY, US); Serra do Caiapó, 5 km S of Caiapônia, 30 Apr. 1973, *W.R. Anderson 9491* (MO, NY, US, W); Serra Dourada, ca 17 km S of Goiás Velho, ca. 6 km NE of Mossamedes, 750 m, 9 May 1973, *W.R. Anderson 9923* (MO, NY, US); Goiás, Niquelandia, ca. de 40 km em direçao a Codemin, 1a entrada antes do posto na placa Rosariana, 15 Jun. 1996, *F.C.A. Oliveira & al. 544* (MO, US); **Maranhão**. Barra do Corda to Grajahú, 1-5 Mar. 1934, *J.R. Swallen 3623* (US); Carolina, 18 Mar. 1934, *J.R. Swallen 3888* (US); Imperatriz, Fazenda Victoria, 6 Aug. 1949, *J.M. Pires & G.A. Black 1696a* (NY); Balsas, 23 Mar. 1994, *B. Nascimento & A.M. de Carvalho 606* (K); **Mato Grosso**. Mato Grosso, in silva primaeva territorio "Praia" dicti, 19-20 Apr. 1894, *O. Malme A.3185b* (G); Mato Grosso, 20 Apr. 1894, *C.A.M. Lindmann 3185b* (P, UPS); Dourados, 4-5 Feb. 1930, *A. Chase 11019* (BM, US, W); Santa Rita do Araguaya on Rio Araguaya, 5-6 Apr. 1930, *A. Chase 11821* (NY); Xavantina-Cachimbo road, 600-1000 m, 31 May 1966, *D.R. Hunt & J.F. Ramos 5673* (K, NY, P, US); Ca. 270 km N of Xavantina, 12°54'S, 51°22'W, 6 Mar. 1968, *D.R. Gifford G71* (NY, P, US); Xavantina-São Felix road, 12°54'S, 51°52'W, 9 Apr. 1968, *J.A. Ratter & al. 939, 2120* (K, MO, NY, P, US); Ca. 30 km S of Xavantina on the Aragarças road, 14 Nov. 1968, *R.M. Harley & R. Souza 11074* (K, MO, P, US); Ca. 30 km ENE of Barra do Garças, 450 m, 5 May 1973, *W.R. Anderson 9777* (C, MO, NY, US); Ca. 5 km N of Barra do Garças, 7 May 1973, *W.R. Anderson 9878* (MO, NY); Cuiabá, Boa Esperança, garden ground of Rua 60, 130-150 m, 16°28'S, 56°02'W, 4 Aug. 1993, *M. Schessl 3410* (MO); Nova Xavantina, ca. 32 km de Nova Xavantina na estrada para Indianápolis, 17 Apr. 2005, *L.P. De Queiroz 10383* (HUEFS); **Mato Grosso do Sul**. 15 km N de Nioaque, Rod. BR-419, 11 Feb. 1993, *G. Hatschbach & al. 58900* (K, NY, W); Bonito, rotovia Bonito-Campos dos Índios, próximo de Três Morros, 10 Mar. 2003, *G. Hatschbach & al. 74460* (K); **Minas Gerais**. Between Uberlandia and Rio Paranahyba, 30 Mar. 1930, *A. Chase 11618* (US); Belo Horizonte, 7 km S of Belo Horizonte, 26 May 1945, *L.O. Williams & V. Assis 7136* (K, MO, NY, US); Serra do Espinhaço, ca. 10 km NE of Francisco Sá, road to Salinas, 1100 m, 12 Feb. 1969, *H.S. Irwin & al. 23138* (US); Serra do Espinhaço, 15 km N of São João da Chapada, 23 Mar. 1970, *H.S. Irwin & al. 28160* (C, US); Serra do Cipó at Cardeal Mota, 1000 m, 19 Feb. 1972, *W.R. Anderson & al. 36296* (C, K, MO, NY, P, US); Serra de Espinhaço, by Rio Jequití 2 km from Mendanha, 13 Apr. 1973, *W.R. Anderson 8787* (K, MO, NY, US); Ca. 15 km W of Pará de Minas along Highway 262 to Uberaba, 760 m, 28 Feb. 1976, *G. Davidse & T.P. Ramamoorthy 10816A* (MO); Joaquim Felicio, entre Varzea da Palma e Joaquim Felicio, 31 km E do Rio das Velhas, 17°35'S, 44°35'W, 12 Feb. 1988, *J.R. Pirani 2154* (NY); Belo Horizonte, Est. Ecologica UFMG, borda de mata, 19 Mar. 1991, *E. Tameirão Neto 439* (MO); Bandeiras, Fazenda Serra Azul, 525 m, 15°49'31"S, 40°31'21"W, 30 Jan. 2004, *W. Thomas & al. 13691* (CEPEC, MO, NY); **Pará**. Conceçao do Araguaia, Alacilandia, 42 km W of Conceiçao do Araguaia along Highway Pa-287, at Rio Arraias do Araguaia, 300 m, 8°13'S, 49°36'W, 23 Feb. 1980, *T.C. Plowman & G. Davidse 9047* (MO, NY, US); Itaituba, estrada Santarém-Cuiabá, BR 163, km 877, Serra do Cachimbo, 8°45'S, 54°57'W, 3 May 1983, *M.N. Silva 214* (MO, NY); **Paraná**. Condrina, near Rolandia, 6-8 Mar. 1946, *J.R. Swallen 8756* (MO, NY); Cascavel, prope flumen Paraná, 10 Jan. 1953, *B. Rambo 53497* (US); Parque Nacional di Iguaçú, 20 Feb. 1960, *E. Pereira 5374* (K); Umuarama, 9 Dec. 1965, *J.C. Lindeman & J.H. & J.H. de Haas 13301* (K, L, NY); Xambrê, 15 Jun. 1966, *J.C. Lindeman & J.H. de Haas 1547* (K, NY); From Icaraima to Pôrto Camargo, 20 Jan. 1967, *J.C. Lindeman & J.H. de Haas 4290* (K, NY, US); Perola, Xambrê, 23 Jan. 1967, *G. Hatschbach 15844* (K, L, US); Barra da Felicidade, 20 Jun. 1967, *G. Hatschbach 16608* (C, K, NY); **Pernambuco**. Caruarú, Serra dos Cavalos, 8°22'S, 36°03'W, 15 Sep. 1981, *J.D.C. Arouck Ferreira 125* (US); **Rio de Janeiro**. Rio de Janeiro, 1835, *E.M. Gaudichaud 303* (FI-Webb); San Pedro, NW of Cabo Frio, 10 Dec. 1929, *A. Chase 10152* (US); Reserva Florestal de Itatiaia, Véu de Noiva, 6 m, 21 Apr. 1972, *P.I.S. Braga 2465* (MO, US); **São Paulo**. Itapira, 13 May 1927, *F.C. Hoehne 20294* (US); 18 km N of Botucatu, along the S. Manuel-Piracicaba Highway, 550 m, 22°45'S, 48°25'W, 22 Apr. 1971, *I.S. Gottsberger 22* (US); São Paulo, Parque do Estado, Feb. 1988, *T. Sendulsky 1990* (HUEFS).

COLOMBIA. Nouvelle Grenade, 1862, *M. Lindig 1044* (MO, P); **Amazonas**. Trapezio amazónico, Loretoyacu River, 100 m, Sep.-Nov. 1944, *R.E. Schultes 6006* (US); Leticia, Parque Nacional Natural de Amacayacu-Inderena, margen izquierdo del Río Amazonas, entre Mocagua y Macedonia, 80 m, 9 Nov. 1990, *X. Londoño & M. Kobayashi 547* (US); **Antioquia**. Vicinity of Medellin, 20 Aug. 1927, *R.A. Toro 377* (US); Fredonia, 1850 m, 3 Aug. 1930, *W.A. Archer 522* (US); In camino between Argelia and Alto del Tigre, 1600 m, 31 May 1944, *E.L. Core 805* (US); Cerca de Santa Elena, camino entre Medellin y Río Negro, 2300-2500 m, 3 Sep. 1946, *J.D. Varela 16* (US); Antioquia, en los alrededores de Dabeiba, 20 Dec. 1947, *F.A. Barkley & G. Gutiérrez 1831* (US); San Luis, 4 km de San Luis, en la via San Luis-Autopista, 760 m, 75°10'W, 6°64'N, 23 Jun. 1987, *R. Callejas & al. 4050* (MO, NY, US); Frontino, km 28.8 of road Nutibara-La Blanquita, region of Murrí, 1020 m, 06°40'N, 76°27'W, 5 Nov. 1988, *J.L. Zarucchi & al. 7174* (K, MO, NY, US); Frontino, road between Nutibara and La Blanquita, region of Murrí, ca. 25 km from Nutibara, 1090 m, 06°40'N, 76°26'W, 8 Feb. 1989, *J.M. McDougal & al. 3757* (BM, MO); Amalfí, Veredas Chorritos, La Maria, Montebello, S-NE de Amalfí, 6°40'-45'N, 74°52'W, 6 Dec. 1989, *R. Callejas & al. 9014* (NY); Cocorná, Vereda La Piñuela, Carretera a San Francesco, 700-800 m, 06°02'N, 75°08'W, 10 Nov. 1991, *D.A. Giraldo Cañas & al. 708* (MO); Maceo, Hacienda Santa Barbara, Parcela de don Cipriano, margen derecha de la quebrada "Guarda sol", 550 m, 6°32'38"N, 74°38'24"W, 20 Nov. 2002, *R. Fonnegra & al. 7731* (MO); **Bolívar**. Badillo, Río Magdalena, 15 Jan. 1913, *F.W. Pennell 3916* (K); Along the Mompos-Juana Sanchez trail. Island of Mompos, Lands of Loba, Apr.-May 1916, *H.M. Curran 223* (MO, NY, US); Fra Squillo, Río Sinu, 90-120 m, 5-6 Mar. 1918, *F.W. Pennell 4605* (NY, US); Vicinity of Turbaco, 200-300 m, 6-22 Nov. 1926, *E.P. Killip & A.C. Smith 14681* (NY, US); **Caldas**. Chinchiná, Jun. 1952, *M. Køie 5311* (C); **Caquetá**. Inter Sucre et Cordoba, 11 Jul. 1925, *G.J.N. Woronow & S. Juzepczuk 5911* (US); Miramar, Río Orteguaza, short way beyond Río Peneya in direction toward Tres Esquinas, 340 m, 16 Jan. 1969, *T.R. Soderstrom 1394* (US); Morelia, Vereda de Santander, quebrada of Río Bodoquero (between Río Pescado and Río Guecochará), 430 m, 20 Jan. 1969, *T.R. Soderstrom 1407* (US), **n = 9!** (Gould and Soderstrom 1970); On road from Florencia to Neiva (near Sucre), 1080 m, 24 Jan. 1969, *T.R. Soderstrom 1413* (K, MO, NY, US); 55 km SE of Guadalupe, 9 Jan. 1974, *G. Davidse & al. 5629* (K), **n = 18!** (Davidse 1978); 15 km SW of Belen along road to San José de Fragua (SW of Florencia), 400 m, 10 Jan. 1974, *G. Davidse 5690* (MO), **n = 18!** (Davidse 1978), *5692* (K, US); 8 km SW of San José del Fragua (SW of Florencia), 11 Jan. 1974, *G. Davidse & al. 5727* (L, MO, NY), **n = 18!** (Davidse 1978); **Chocó**. Hoya del Río San Juan, Andagoya, 5°06'N, 76°42'W, 13 Apr. 1979, *E. Forero & al. 5173* (MO); Pizarro, margen izquierdo del Río Pepé, entre Boca de Pepé y Pié de Pepé, 19 Nov. 1985, *J. Espina 2010* (MO); Tadó, cerca de Agua Clara, 6 Dec. 1990, *J.L.F. Alonso & al. 8558* (FI, MA); **Cundinamarca**. Bayo Magdalena, Perrero, 17 May 1926, *G.J.N. Woronow & S. Juzepczuk 4868* (US); Cercanias de San Bernardo, hacia Sasaima, 1800-1900 m, 23 Jun. 1940, *J. Cuatrecasas 9624* (US); Abajo de Cachpay, camino que va a la hacienda "Las Mesitas", 1620 m, 3 Nov. 1941, *G. Gutierrez 128* (NY, US); Quebrada Carmargo, N of Apulo, 460-480 m, 5 May 1944, *E.P. Killip & al. 38230* (US); 20 km NW of Villavicencio along the road to Bogotá, 800 m, 3 Jan. 1974, *G. Davidse & F. Llanos 5522* (K, MO, US), **n = 18!** (Davidse 1978); Poblado de Nariño, carretera de los Mmangos, 15 Feb. 1986, *J.L.F. Alonso & R. Jaramillo 5277* (FI, MA); **Huila**. Inter Guadelupe et La Resina, 8 Jul. 1926, *G.J.N. Woronow & S. Juzepczuk 5744* (US); 2-3 km above Finca Cedral, valley of Río Fortalecillas, 32-33 km E of Neiva, 1500 m, 2°58'N, 74°57'W, 18 Jan. 1943, *F.R. Fosberg 19777* (US); Huila, 25 Aug. 1944, *J.R. Swallen 1947* (K); 10 km SE of Guadalupe along road to Florencia, 1040 m, 9 Jan. 1974, *G. Davidse & al. 5605* (K, MO, US), **n = 18!** (Davidse 1978), *5629* (MO, US), *5585A* (MO); 6 km SE of Altamira along road to Florencia, 9 Jan. 1974, *G. Davidse & al. 5585A* (K); **Magdalena**. Santa Marta, 1898-1901, *H.H. Smith 2147* (G, MO, NY, P, US), *H.H. Smith 2148* (BM, G: *pro parte*; K, L, MO, NY, P, US: *pro parte*), *H.H. Smith 2258* (MO: *pro parte*), Jul. 1903 *H.H. Smith 2531* (K, NY); **Meta**. Near "Casa Papamene", floor of valley of Río Papamene, Colombia-Uribe trail, 770 m, 3°12'N, 74°33'W, 23 Dec. 1942, *F.R. Fosberg 19519* (US); Meta, Sierra de La Macarena, 13 Mar. 1956, *J.M. Idrobo & R. Jaramillo 2176* (NY); Floodplain of Río Metica just E of Puerto Lopez, 210 m, 1 Jan. 1974, *G. Davidse & F. Llanos 5469* (MO, US); Llanos area 4 km NW of Villavicencio towards Bogotá, 1130 m, 10 Jan. 1976, *J.L. Luteyn 4799* (MO, NY, US); Villavicencio, Sitio Piperal, 27 Feb. 1987, *L. Quiñones 982* (MO); Km 18 de la vía Granada-San Juán de Arama, 495 m, 16 May 1987, *X. Londoño & I. D. Quintero 283* (US); **Nariño**. Inderena Station, km 55 from Timaco on road to Tuquerres, 23 Nov. 1981, *A. Gentry & al. 34876* (MO); Tumaco, Río Chapul, 30 m, 78°28'W, 1°46'26"N, 19 Jun. 1989, *B. Madrigal & al. 679* (MO, NY); **Norte de Santander**. Between Chinacota and La Esmeralda, 1000-1300 m, 19 Mar. 1927, *E.P. Killip & A.C. Smith 20901* (US); Norte de Santander, Region del Sarare, Hoya del Río Chitagá entre Corro Colorado y Bata, 1300 m, 14-17 Oct. 1941, *J. Cuatrecasas & al. 12239* (US); **Putumayo**. Mocoa, corregimiento de San Antonio, vereda Alto Campucana, finca La Mariposa, 1320-1420 m, 01°12'N, 76°38'W, 20-21 Apr. 1994, *J. Betancur & al. 4975* (MO); **Santander**. Northern slope of Mesa de Los Santos, 1000-1500 m, 11-15 Dec. 1926, *E.P. Killip & A.C. Smith 14992* (NY, US); Upper Río Lebrija, NW of Bucaramanga, 400-700 m, 29 Dec. 1926, *E.P. Killip & A.C. Smith 16302* (US); Río Altura, 700 m, 21 Dec. 1948, *A. Molina & al. 18 N.S. 070* (K, US); Ca. 10 km S of Socorro, 6 Nov. 1984, *J.R. Wood 4583* (K, MO, US); **Tolima**. "La Trinidad", Libano, 110-1400 m, 21-25 Dec. 1917, *F.W. Pennell 3225, 3237* (MO, NY, US); Río Coello, New Quindio Trail, 100-1500 m, 13 Aug. 1922, *E.P. Killip 9732* (US); Ibaqué, 8 May 1932, *J. Cuatrecasas 2996* (MA); W of Chaparral, ca. 5 Km, 900 m, 29 Jul. 1950, *S.G. Smith 1295* (US); On the Quindio pass, ca. 2 km below Cajamarca, 1600 m, 2 Nov. 1983, *J.R. Wood 4088* (K, US); **Valle**. El Valle, Cordoba, 80-100 m, wooded cliffs of Río Dagua, 6-8 May 1922, *E.P. Killip 5052* (US); Río Agua Bonita to Río Vieja, E of Zarzal, 1300-1400 m, 23 Jul. 1922, *F.W. Pennell & al. 8567* (NY, US); Cali, Cerro de las Cruces, 26 May 1932, *J. Cuatrecasas 2008* (MA); El Valle, Hacienda "El Trjo", N of Palmira (Cauca Valley), 1050 m, 28 Dec. 1938–5 Jan. 1939, *B.H. Garcia 6458* (US); El Valle, Río Digua Valley, 675 m, 2-4 Apr. 1939, *E.P. Killip 34837* (BM, US); El Valle, Cordillera Occidental, hoya del Río Calima, El Cairo, entre Darién y Mediacanoa, 1650-1750 m, 6-7 Jan. 1943, *J. Cuatrecasas 13884* (US); Cordillera Central, Hoya del Rio Digua, Piedra de Moler, 900-1180 m, 19–28 Aug. 1943, *J. Cuatrecasas 15069* (P); El Valle, Cali, 1000 m, 3°27'N, 76°30'W, 30 Jun. 1944, *F.R. Fosberg 21990* (US); El Valle, La Cumbre, 1680 m, 26 Feb. 1945, *J. Cuatrecasas 19617* (US); Cordillera Occidental, Cali, Loma Los Cristales, 1300-1400 m, 25 Dec. 1959, *J. Cuatrecasas & al. 25693* (US); El Valle, Tuluá, Mateguadua, Jardin Botanico, 1100 m, Apr. 1978, *H. Cuadros V. 440* (MO); El Valle, Hacienda San Gerardo, cerca de Guabas, muy cerca de frontera con Guacarí, parte plana del Valle del Río Cauca, 950 m, 19 Dec. 1987, *F.A. Silverstone-Sopkin & al. 3396* (MO); El Valle, Yotoco, Hacienda San Martin, ca. 1 hora de Media Canoa, 11 Nov. 1990, *J.E. Ramos & L.H. Ramos 2909* (MO); Cauca, Km 5 on the Mojarras-Mercaderes road, 1000 m, 77°12'W, 1°50'N, 3 Feb. 1988, *X. Londoño & L.G. Clark 373* (MO, US); Yumbo, Corregimiento de Mulaló, 3 km arriba del pueblo de Mulaló, por la Carretera del oleoducto del Pacifico, Carretera Panorama, 1300 m, 1 May 1990, *J.E. Ramos & al. 2706* (MO); **Vichada**. Ca. 8 km E of Las Gaviotas along road to Santa Rita, 25 Dec. 1973, *G. Davidse & F. Llanos 5165* (K, MO); Vichada, ca. 35 km E of Las Gaviotas along unimproved dirt road to Santa Rita, 170 m, 26 Dec. 1973, *G. Davidse & F. Llanos 5198* (K, MO, US).

COSTA RICA. **Alajuela**. Entre Ríos Itiquis y Poas, 29 Oct. 1933, *A.M. Brenes 17331* (NY); San Miguel de San Ramon, 19 Jan. 1937, *A.M. Brenes 21959* (NY); 1 km N of Atenas, 700 m, 31 Oct. 1968, *R.W. Pohl & G. Davidse 11365* (US); Valley of Río Itiquis, ca. 4 km W of Alajuela, 800 m, 2 Dec. 1970, *G. Davidse & R.W. Pohl 12544* (MO); Along Río Capote about 1 km from the small town of Capote, 10°45'N, 85°05'W, 5 Jan. 1975, *J. Taylor 18156* (NY, US); Between Cerro Chato and Cerro de los Perdidos, 17 Feb. 1989, *G.F. Russell & al. 769* (NY, US); Guatuso P.N. Volcán Tenorio, Cuenca del Río Frio, Alto Masis, 1200 m, 10°40'17"N, 84°59'25"W, 23 Jan. 2002, *J.L. Chaves 1409* (MO); **Cartago**. San Rafael de Cartago, 28 Aug. 1892, *H. Pittier 7110* (G); Atirro, Mar. 1894, *J. Donnell Smith 4891* (US), *4991* (K, US); Tuqurrique, Dec. 1898, *A. Tonduz 12858* (BM, G, L, P, US); Bouissons á Las Vueltas, Dec. 1899, *A. Tonduz 12858* (G); Nicoya, Jan. 1900, *A. Tonduz 13755* (BM, G, K, P, US); Vicinity of Pejivalle, 7-8 Feb. 1924, *P.C. Standley & J. Valerio 47060, 46876, 47168* (US); Vicinity of Orosi, 30 Mar. 1924, *P.C. Standley 39648* (C); Vicinity of Pejivalle, Jan. 1940, *A.F. Skutch 4631* (MO, NY, US); **Guanacaste**. Vicinity of Cañas, Finca La Pacifica, 16 Dec. 1969, *R. Daurenmire 438* (USJ); Guanacaste, edge of Bosque Humedo ca. 1 km E of HQ of Santa Rosa Natural Park, 290 m, 25 Jan. 1983, *E.J. Judziewicz 4283* (MO); Canton de La Cruz, P.N. Guanacaste, Cordillera, Estación Pitilla, 460-600 m, 11°01'35"N, 85°25'45"W, 20 Jan. 1996, *C. Moraga 686* (MO); **Limón**. Barra del Colorado, N side between town and ocean beach, sea level, 10°47'N, 83°35'W, 26 Jan. 1986, *W.D. Stevens 24108* (MO); **Puntarenas**. Forets de Boruca, Nov. 1891, *H. Pittier 4455* (G, P, US, W); Vicinity of La Palma, on the road to La Hondura, 17-18 Jul. 1923, *W.R. Maxon & Harvey 8050* (C); Peninsula Osa ad Golfo Dulce, circa Puerto Jimenez, 10 Apr. 1930, *G. Cufodontis 180* (US, W); San Vito de Java, Aug. 1964, *H.S. McKee 11182* (K, P, US); 20 miles NW of Golfito, 27 Feb. 1965, *E.W. Lathrop 5580* (K); Peninsula de Osa, 28 Feb. 1965, *R.K. Godfrey 66850* (US, USJ); Near Finca Las Cruces near San Vito de Java, 28 Jul. 1968, *R.W. Pohl & G. Davidse 10790* (K, US), **n = 18!** (Davidse 1978); Buenos Aires, sabanas de Paso Real, 20 Dec. 1976, *J. Gómez Laurito 1068* (USJ); La Vaca, frontiera sur, 22 Dec. 1976, *J. Gómez Laurito 1082* (USJ); Reserva Biologica Carara, sendero Quebrada Bonita a Bijagual, 8 Dec. 1980, *R. Zúñiga 8* (K); Parque Nacional Corcovado, Dos Brazos de Río Tigre, Jimenez, Cuenca superior del Río Madrigal, 600 m, 8°29'50"N, 83°28'55"W, 1 Dec. 1990, *G. Herrera 4735* (MO); Cantón de Osa, Los Mogos, 20 m, 8°45'00"N, 83°22'50"W, 14 Jan. 1991, *E. Castro 100* (USJ); forests along S side of Quebrada Bonita, to ca. 1 km E of Costanera Highway, Carara Reserve, 30-40 m, 9°47'N, 84°37'W, 11 Jan. 1985, *M. Grayum 4737* (MO); Puntarenas, Buenos Aires, Parque Nacional de La Amistad, Cuenca Térraba-Sierpe, 9°07'07"N, 83°05'07"W, 1600-1700 m, 24 Feb. 2008, *A. Rodriguez 11939* (PMA); Reserva Forestal Golfo Dulce, cerca Banegas Los Charcos, 8°40'18"N, 83°30'17"W, 49 m, 29 Dec. 2008, *R. Aguilar 11679* (NY); **San José**. Vicinity of El General, Dec. 1935, *A.F. Skutch 2189* (K, MO, NY, US); Vicinity of El General, 670 m, Jan. 1939, *A.F. Skutch 3817* (US), *3875, 3876* (MO, NY, US); Lower slopes of Cordillera de Talamanca, along Río Hermoso, Finca El Quizarrà, 28 Jan. 1965, *L.O. Williams & al. 28449* (MO, NY, US).

CUBA. **Oriente**. Oriente, Sierra de Nipe, on limestone foothills near Sabana La Burra, 13 Nov. 1919, *E.L. Ekman 10095* (G, NY, US); Oriente, Sierra de Nipe, Picote, on the southern slope, 14

Nov. 1919, *E.L. Ekman 10108* (US); Oriente, Papato, of the Sevilla tract, 11 Jan. 1920, *E.L. Ekman 10318* (US); Oriente, Sierra Maestra, Pinar de Bangamita, 12 Jan. 1920, *E.L. Ekman 10324* (G, US); Woods SE of Soledad, 30 Nov. 1926, *A.S. Hitchcock 23325* (US); **Santa Clara**. Hoyo de Manicaragua, 26-28 Feb. 1910, *N.L. Britton & al. 4694* (NY); Rincon to Banao, 3 Mar. 1912, *J.A. Shafer 12323* (BM, NY, US); Banao Mts., 1921, *A. Luna 1007* (NY); Lomas de Piguanca al Río Navarro, 3 Jun. 1922, *E.L. Ekman 13878* (US); San Blas, La Sierra, 8 Mar. 1929, *J.G. Jack 7053* (NY); San Blas-Buenos Aires, Trinidad Mountains, 6 Jan. 1942, *A. Gonzales 469* (MO, P, UPS, US).

DOMINICAN REPUBLIC. Santo Domingo, Jan.-Mar. 1871, *C. Wright & al. 614* (US); **Barahona**. Trail between Monteada Nuevo and La Lanza, 31 Jul. 1950, *R.A. Howard 12237* (BM, NY); 2 km norte de Paraiso, camino hacía Villa Niza, Valle de Río Nizaito, 18°00'N, 71°10'W, 3 Dec. 1981, *M. Mejía & J. Pimentel 18396* (FTG); **La Altagracia**. Isla Saona, 8 Jul. 1956, *Prof. Marcano & J. de Jesus Jiménez 3371* (US); **La Vega**. Cotuy, sea level to 300 m, 28 Jan. 1921, *W.L. Abbott 737* (US); Cerca de Río Grande, Constanza, 22 Oct. 1950, *J. de Jesus Jiménez 2123* (US); Between La Vega and Jarabacoa, 17 Mar. 1957, *J. de Jesus Jiménez 3468* (US); Jarabacoa, 4 May 1963, (NY); 12 km S of La Vega along the Santiago-Santo Domingo Highway, 150 m, 14 Aug. 1970, *G. Davidse 2680* (MO); Cabirma de La Loma, 20 Jun. 1973, *A.H. Liogier 18799* (NY); Loma del Puerto, Jarabacoa, 25 Jan. 1976, *A.H. Liogier 24732* (NY); Falcombridge Dominicana mine property, N of Río Yuna, N of Bonao, lowland broadleaf forest at base of Loma El Caribe, at W side in area called Jayaco relatively undamaged, 18°59'N, 70°25'W, 22 Apr. 1981, *T. Zanoni & al. 12877* (NY); La Vega, 7.7 km N of Buena Vista, 340 m, 19°12'N, 70°34'W, 10 Jan. 1991, *S.A. Thompson 8230* (MO). **Samaná**. Vicinity of Laguna, Samaná Peninsula, chiefly on the Pilón de Azucar, 100-500 m, 19 Dec. 1920, *W.L. Abbott 332* (US); **San Juan**. Pietra del Aguacate to Río del Oro, 12 Oct. 1946, *R.A. Howard 9454* (BM, FI, NY, US); **Santiago**. Cordillera Central, Loma Diego de Orampo, 19 Jul. 1929, *E.L. Ekman 13200* (US); San José de las Matas, 24 Dec. 1929, *E.J. Valeur 307* (MO, US); Vicinity of Santiago, 200-500 m, 11 Jan. 1946, *H.A. Allard 14557* (US); Loma del Puerto, on road to Hotel Montaña, 9 Apr. 1964, *F.W. Gould & J. de Jesus Jiménez 10892* (US); Cordillera Septentrional, sobre Loma El Murazo, 19°41'N, 70°58'W, 18 Dec. 1984, *T. Zanoni & al. 32876* (MO, NY); Cordillera Central, en el poblado rural de Las Lagunas de Cenocì, 19°15'N, 71°18'W, 30 Nov. 1989, *T. Zanoni & al. 44044* (NY); **Santiago Rodriguez**. Aguacate, Moncion, Nov. 1974, *G. Jürgens 6391B* (MO); **Santo Domingo**. Llanos Costero, St. Domingo City, 14 Jan. 1929, *E.L. Ekman 11157* (US); Santo Domingo City, banks of Río Ozama, 14 Dec. 1929, *E.L. Ekman 14219* (G, K, US); Vicinity of Ciudad Trujillo, 19 Nov. 1945, *H.A. Allard 13452* (NY); El Torito, Yuna, Rancho Arriba, 750 m, 20 Nov. 1976, *A. & P. Lioger 26054* (FTG); Llanura Costiera, Distr, Nacional, Sierra Prieta en el poblado de Sierra Prieta, 18°39'N, 69°58'W, 8 Nov. 1984, *T. Zanoni & al. 32050* (NY); Nacional, base and lower southern slope of Sierra Prieta, 13.7 km N of Villa Mella, 14 Dec. 1986, *R. Carter & R. Garcia 5321* (MO).

ECUADOR. Ecuador, s.d., *H.F.A. von Eggers 15006* (K, L), *15421* (K); **Carchi**. Perhumid forest on wet plateau above San Marcos de los Coaiqueres, on trail towards Gualpí Bajo, 1000 m, 78°17'W, 01°06'N, 7 Feb. 1985, *S. Lægaard & al. 57466* (MO, UPS); Carchi-(Esmeraldas) wet evergreen forest, near Lita, 600 m, 19 May 1987, *H. van der Werff & al. 9494* (MO); **Chimborazo**. Huigra, 1200 m, 16 Jul. 1923, *A.S. Hitchcock 20607* (US); Río Chanchan near Huigra, 14 May 1945, *W.H. Camp E-3039* (K, P, US, W); Road General Elizalde (Bucay)-Pallatanga, 32 km from Pallatanga, 650 m, 79°02'W, 2°09'S, 29 Aug. 1976, *B. Øllgaard & H. Balslev 8994* (MO, NY); **Cotopaxi**. Road between Quevedo and El Corozon, 1.9 km NW of El Corozon, 67.5 km SE of Quevedo, 1225 m, 01°07'S, 79°06'W, 5 Apr. 1983, *T.B. Croat 55821* (MO); Km 60 Quevedo-Latacunga, 1150 m, 11 Mar. 1988, *S. Lægaard* 71257 (G), *S. Lægaard 70774* (K); **Esmeraldas**. Quinindé, 21 Aug. 1950, *M. Acosta Solís 19613* (US); Virgin forest long trail Río Lita, 22 Jul. 1964, *C. Játiva & C. Epling 889* (NY); Hacienda Timbre, Hacienda Guayas, 20 km S Esmeraldas, 14 Apr. 1967, *B. Sparre 15516* (UPS); Lita-San Lorenzo road, 10 km NW of Lita, 800 m, 00°55'S, 78°35'W, 11 May 1991, *A. Gentry & al. 70169* (MO); **Guayas**. Guayaquil, 18-20 Jun. 1923, *A.S. Hitchcock 20133* (NY); Milagro, 30 Jun.-2 Jul. 1923, *A.S. Hitchcock 20295* (NY), *20236* (NY, US); Teresita, 3 km W of Bucay, 270 m, 5 Jul. 1923, *A.S. Hitchcock 20432* (US); Guayaquil, 26 Apr. 1939, *E. Asplund 5802* (FI, K, NY, P, UPS, US), *5810* (G, US); Bucay, 12 Aug. 1943, *M. Acosta Solis 5216* (US); Guayaquil, Cerro Azul, 29 Apr. 1959, *G. Harling 4836* (UPS); Cerro de Isera, Julio Moreno, 23 Jul. 1962, *C. Játiva & C. Epling 155* (NY); Capeira, km 21 Guayaquil to Daule, 20-200 m, 19 Sep. 1981, *C.H. Dodson & P.M. Dodson 11398* (MO); Guayaquil Canton, Carretera a salinas, km 15, 350 m, 02°10'S, 79°58'W, 15 Aug. 1991, *D. Rubio & al. 1776* (MO); Naranjal, Parroquia Taura, Reserva Ecológica Manglares-Churute, Cerro Perequetre Chico, 160-300 m, 02°27'S, 79°40'W, 26 Feb. 1992, *C.E. Cerón & al. 18279* (MO); **Imbabura**. 14 km W of the town of Apuela on the road to Selva Alegre, 1250 m, 16 Mar. 1980, *S.M. Young 75* (US); **Loja**. Cerro Gordo (Zaruma), 12 Aug. 1947, *R. Espinosa 1726* (K), 18 Aug. 1947, *R. Espinosa 1780* (US); Rio Comunidades, between Vilcabamba and Yangana, along the river, 14 May 1967, *B. Sparre 16128* (P); Macara-Catacocha, 4°22'S, 79°57'W, 1100 m, 11 May 1988, *S. Lægaard & E. Kullberg 71223* (G); Las Chinchas-Portovelo ca. 18 km below Zumbe, 4 Jun. 1999, *S. Lægaard & al. 20237* (K); **Los Ríos**. Hacienda Clementina on Río Pita, 27 Mar. 1939, *E. Asplund 5494* (MO), *5496* (G, K, NY); Pichilingue, Cantón Ouvedo, 1 Aug. 1945, *M. Acosta Solis 10696* (US); Hacienda Clementina, 30 m, 10 Feb. 1947, *G. Harling 256* (US); 21 km S of San Carlos and 69 km N of Babahoya, 17 Feb. 1974, *A. Gentry 9992* (MO); On slopes and ridges near Río Palenque, Biological Station, between river and Pan Am Highway to Santo Domingo de los Colorados, 54 km N of Quevedo, 180 m, 00°38'S, 79°24'W, Jun.-Jul. 1977, *H.H. Iltis & M.G. Iltis 130* (MO, US); Quevedo Canton, Parroquia Centinela-La Piramide, Via Santo Domingo de Los Colorados-Quevedo entrando por Patricia Pilar km 41, 650 m, 01°40'S, 79°20'W, 25 Feb. 1992, *C. Quelal & G. Tipaz 264* (MO); **Manabí**. Ca. 20 km S of Jipijapa, 8 Mar. 1988, *S. Lægaard 70682* (K); **Morona-Santiago**. Along road S of Gualaquiza, 1000-1100 m, 78°33'W, 03°24'S, 3 Apr. 1985, *S. Lægaard 53994* (K, MO); Alrededores del puente sobre el Río Bombiozaen la carretera Gualaquiza-Zamora y cerca la Paroquia de Bomboiza, 800 m, 26 Aug. 1985, *M.A. Baker 6307* (MO); Kankaim, 15 Sep. 1985, *K.S. Lowell 488* (NY); Centro Shuar Yukutais, 10 km S Sucua, Río Upano, 02°31'S, 78°09'W, 28 Sep. 1988, *P. Gomez 499* (MO, NY); Vieja Cordillera de Cutucù, km 19 on Mendez-Morona road paralleling the Río Namangoza, 2°43'S, 78°19'W, 16 Jun. 1989, *L.J. Dorr & I. Valdespino 6298* (NY); Morona Canton, Cordillera del Cutucú, Comunidad Angel Ruby, Pie de la Cordillera, 1064 m, 02°21'41"S, 78°02'24"W, 26 Mar. 2002, *L. Suin & al. 1266* (MO); **Oro**. Between La Chorita and Portovelo (Golden Mine near Zaruma), 1000-2000 m, 28 Aug. 1923, *A.S. Hitchcock 21196* (US); Leon, near Santa Rosa, Canton Pjili, 1000 m, 17-20 Nov. 1934, *Y. Mexia 6725* (BM, US); **Napo**. Napo-(Pastaza), vicinity of Puyo, 750-1000 m, Aug. 1939, *A.F. Skutch*

4392 (K, MO, NY, US); Puerto Francisco de Orellana (Coca), 300 m, 76°52'W, 00°40'S, 4 Nov. 1976, *H. Balslev & E. Madsen 10593* (MO, NY); Road Coca-Auca oilfields, 3 km along the road to Yucca, 76°55'W, 00°28'S, 20 Aug. 1979, *L. Holm-Nielsen & al. 19624* (MO, NY); Cotundo, 18 May 1972, *H. Lugo 2357* (K, MO, NY); Morona-Santiago, road Sucua-Macas, 750 m, 24 Sep. 1979, *L. Holm-Nielsen & al. 20469* (K, US); 35 km N of Tena on the road to Baeza, 1150 m, 25 Mar. 1980, *S.M. Young 83* (MO, US); San Pablo at Río Aguarico, 5 May 1984, *S. Lægaard 52077* (K); Napo, Río Napo below Mishauali, 14-15 Dec. 1985, *S. Lægaard 55839* (K); Reserva Biologica Jatun Sacha, 8 km de Puerto Misahuallì, 450 m, 01°04'S, 77°36'N, 4 Sep. 1987, *C.E. Cerón & M. Cerón 2118* (MO, NY); Km 35 from junction Baeza-Tena road to Loreto, 77°36' W, 0°40'S, 25 May 1988, Estación Biologica Jatun Sacha, 450 m, 01°04'S, 77°36'W, 24 Aug. 1988, *C.E. Cerón & M. Cerón 4609* (MO); **Pastaza**. Colonia 24 de Mayo, side road to road to Puyo-Puerto Napo, 27 Jun. 1972, *H. Lugo 2497* (K, NY); Río Capahuari, ca. 12 km N of Puerto Sarayacu, 13 Aug. 1974, *H. Lugo 4114* (K, MO, NY); Near Puyopungu, 24 Nov. 1976, *H. Lugo 4985* (K, NY); Pacayacu on the Río Bobonaza, ca. 16 km NW of Sarayacu, 10 Aug. 1979, *H. Lugo 5211*, 12 Aug. 1979, *H. Lugo 5311* (K, MO, NY); Río Bobonaza, Quilloallpa, below Montalvo, ca. 300 m, 76°53'W, 2°10'S, 17 Jul. 1980, *B. Øllgaard & al. 34583* (K, MO, NY); Montalvo, on the Río Bobonaza, 300-350 m, 76°58'W, 2°5'S, 28 Jul. 1980, *B. Øllgaard & al. 35473* (K, MO, NY); Road Puyo-Macas, 2 Dec. 1984, *S. Lægaard & al. 53403* (K); Río Curaray, costado sur, boca del Río Querano, 230 m, 01°30'S, 76°32'W, 3 Sep. 1985, *D. Neill & W. Palacios 6840* (MO); Cantón, Simon Bolívar, bosque Protector Arutam, Km 47 on Puyo-Macas Highway, 01°46'53"S, 077°49'57"W, 800-950 m, 10 Aug. 2005, *J.L. Clark et al. 9117* (NY); **Pichincha**. Puente Gloria de Maria, W of Quito, 1200 m, 27 Jun. 1939, *E. Asplund 7272* (US); Between Chiriboga and Santo Domingo de los Colorados, 2000 m, Dec. 1952, *F. Fagerlind & G. Wibom 1961* (US); Road El Paraiso-Saguangal, 11 km from El Paraiso, 1200 m, 78°46'W, 0°12'N, 2 May 1982, *B. Øllgaard & al. 37710* (MA, MO, NY); NE of Vicente Maldonado, Reserva de ENDESA, 600 m, 79°02'W, 00°06'N, 7-10 Jul. 1984, *S. Lægaard 52471* (K, MO, NY, UPS); NE of Alluriquin, 1050 m, 00°19'S, 78°59'W, 21 Jul. 1985, *S. Lægaard 54712, 54713* (K, MO, NY, UPS); Carretera Quito-Chiriboga-Empalme, 1200-1300 m, 00°15'S, 78°50'W, 13 Dec. 1987, *V. Zak & J. Jaramillo 3206* (K, MO, NY, US); Canton Quito, Parroquia Nanegal, Reserva Maquipucuna, El Pacchal, N of Hacienda El Carmen, 1350 m, 00°08'N, 78°38'W, 7 Jan. 1995, *G.L. Webster 31039* (MO); **Santiago-Zamora**. Near Mendez, 1750-2500 ft, 5-6 Nov. 1944, *W.H. Camp 911* (US); **Tungurahua**. Valley of Patata River, between Banhos and Cashurco, 8 hours east of Banhos, 25 Sep. 1923, *A.S. Hitchcock 21808* (US); Valley of Río Pastaza, between Machai and La Victoria, ca. 1400 m, 24 Aug. 1939, *E. Asplund 8512* (MO); En e camino de Baños a Rioverde, entrada al Oriente, 10 Jul. 1945, *M. Acosta Solis 10263* (US); Along road from Río Negro to La Estancia and Parque Nacional Sangay, 1.8 km S of bridge over Río Pastaza, 1335 m, 01°25'24"S, 78°13'01"W, 4 May 2003, *T.B. Croat & al. 88484* (MO); **Zamora-Chinchipe**. 15,5 km N of Zumba on road to Loja, 1250 m, 1 Jun. 1990, *P.M. Peterson & E. Judziewicz 9439* (US); Ca. 15 km N of Yantzaza, 900 m, 3°49'S, 78°46'W, 15 Jun. 1998, *S. Lægaard 18895* (K, MO); El Pangui, Cordillera del Condor, arriba del valle del Río Quimi, 1300 m, 03°30'26"S, 78°25'15"W, 11 Dec. 2000, *J. Caranqui & al. 177* (MO); Along road from Zamora to Janeiro, vicinity of municipal garbage dump, along Quebrada Janeiro, 1.3 km NW of Bridge over Quebrada Janeiro, 1009 m, 4°02'53"S, 78°57'51"W, 22 Jul. 2004, *T.B. Croat 91906* (MO); Zamora, Cordillera del Condor, Parroquia San Carlos de Las Minas, Nambija, San Carlos, 1100-1500 m, 04°00'54"S, 078°50'11"W, 30 Jan. 2005, *W. Quizhpe & al. 857* (MO, US); Vicinity of Ecuacorrientes mining company, Valley of Río Quime, trail along Río Waiwaime near its mouth at Río Quima, 1000 m, 03°33'45"S, 78°27'47"W, 23 Sep. 2007, *T.B. Croat & G. Ferry 99051* (MO).

EL SALVADOR. **San Salvador**. West side of Lake Ilopango, 23 Nov. 1911, *A.S. Hitchcock 8921* (NY, US); Tonacatepeque, 1922, *S. Calderón 509* (NY, US); San Salvador, 30 Mar.-24 Apr. 1922, *P.C. Standley 23117* (US); Lomas de Candelaria, 1929, *S. Calderón 2514* (K, US); Cabañas, A.P. Cinquera, La Torre y Campamento La Cascabel, 380 m, 13°53'N, 88°57'W, 23 Dec. 1997, *S. Henriquez & M. Cartagena 5174* (MO).

FRENCH GUIANA. s.l., 1842, *M. Melinon 397* (L, P, US); Route de Kourou, 1 Sep. 1955, *J. Hoock 83* (NY, P), *375* (CAY, US); Saül, 30 Jun. 1956, *J. Hoock 91* (CAY, P); Prés de Maripasonda, 1 Sep. 1961, *R. Schnell 11692* (US); Saül Region, along road between airport and Saül, 3°37'N, 53°12'W, 29 Oct. 1986, *L. Skog & C. Feuillet 7106* (CAY, NY); Savane Renner, 3 m, 52°53'N, 5°20'W, 18 Apr. 1996, *G. Cremers & J.J. de Granville 14455* (CAY); Mana, route d'Awala, 4 m, 53°48'0"N, 5°41'0"W, 20 Sep. 1999, *J.J. de Granville & F. Croizer 13812* (CAY); Monts d'Arawa, savane-roche centrale, 200 m, 53°22'00"N, 02°49'00"W, 11 Jul. 2002, *J.J. de Granville et al. 15207* (CAY); Mount Saint-Marcel, 27 Jul. 2002, *J.J. de Granville & al. 15518* (CAY, K); Inselbergs de la haute Wanapi, zone du dôme central, 170 m, 53°49'20"N, 02°31'00"W, 13 Apr. 2004, *J.J. de Granville et al. 15880* (CAY); Inselbergs du haut Marouini, Inselberg de la D.Z., 190 m, 2°36'30"N, 54°1'45"W, 21 Jun. 2004, *J.J. de Granville & F. Croizer 16318* (CAY); Saül, Crique Limonade dans les environs de la confluence avec la Crique Cochon, 180 m, 03°34'36"N, 53°12'48"W, 11 Dec. 2007, *O. Tostain et al. 1128* (CAY).

GUATEMALA. s.l., 1841, *E. Ritter von Friedrichsthal 549* (FI); **Baja Verapaz**. 16 miles from Salamá, 11 Nov. 1958, *J.G. Hawkes & al. 1921* (C, G, K); **Copán**. Pietra Blanca de Qualán, Jan. 1907, *H. Pittier 1787* (US); Livingstone, Río Dulce, 1889, *D. Smith 1852* (K); **Guatemala**. Guatemala City, 1-3 Dec. 1911, *A.S. Hitchcock 9036* (NY), *9053* (US); Damp wooded barranco 10 km S of San Raimundo, 18 Jan. 1939, *P.C. Standley 62914* (US); **Izabal**. Los Amates, 15 Feb. 1908, *W.A. Kellerman 7472* (NY, US); Quirigá. 2 Mar. 1932, *P. Weatherwax 94* (K); **Petén**. forest between Finca Yalpemech along Río San Diego and San Diego on Río Cacuen, 50-150 m, 25 Mar. 1942, *J.A. Steyermark 45402* (US); Petén, Dolores, E of village on Río Mopan trail, 12 May 1961, *E. Contreras 2283* (US); Petén, Tikal, 2 Mar. 1974, *W.C. Verboom 5035* (K); **Sacatepéquez**. Alotenango, 1300 m, 11 Nov. 2004, *M. Véliz 1586* (MO).

GUYANA. **Berbice-Corentyne**. Oreala, Corentyne River, Oct. 1879, *G.S. Jenman 256* (K, US); **Potaro-Siparuni**. Pakaraima Mts., Upper Ireng R. watershed, Malakwalai-Tipu summit on narrow ridge to SE escarpment, 1400 m, 04°48'N, 60°18'W, 13 Jul. 1994, *T.W. Henkel 5590* (CAY, MO, US); **Rupununi**. Western extremity of Kanuku Mts., 4-22 Mar. 1938, *A.C. Smith 3314* (G, K, MO, NY, P, US, W); Western extremity of Kanuku Mountains, in drainage of Takutu River, dense forest, 4-22 Mar. 1938, *A.C. Smith 3131* (G); 1 mile S of Emprensa, 500 ft, 14 Sep. 1963, *R. Goodland 715* (K, NY, P, US); Kanuku Mts., slope of Nappi Mt., 450 m, 03°20'N, 059°34'W, 8 Nov. 1987, *M.J. Jansen-Jacobs & al. 758* (CAY, K, MO, NY, US); Kanuku Mts., Maipama, 160 m, 03°22'N, 059°30'W, 17 Nov. 1987, *M.J. Jansen-Jacobs & al. 966* (K, US); Kanuku Mts., slope of Bank of Guyana, 140-320 m, 03°21'N, 059°29'W, 26 Nov. 1987, *M.J. Jansen-Jacobs 1274* (CAY, US); Karanambo, 3°45'N, 59°20'W, 1 Sep. 1988, *P.J.M. Maas & al.*

7150 (CAY, K, NY, US); Eastern Kanuku Mts., NE of Warimure, 200-500 m, 03°05'N, 059°20'W, 23 Jan. 1991, *M.J. Jansen-Jacobs 2182* (CAY, K, MO, NY, P, US); Kanuku Mts., Crabwood Creek, 03°07'N, 059°06'W, 25 Jan. 1994, *M.J. Jansen-Jacob & al. 3346* (CAY, K, MO, NY, P); NE slope of Mount Shiriri, 450 m, 02°53'N, 059°43'W, 18 Jun. 1995, *M.J. Jansen-Jacobs & al. 4149* (US); **Upper Takutu-Upper Essequibo**. SE Kanuku Mts., Makaparima Mtn., foothills, 4 km NNE of Crabwood Creek camp, 400-450 m, 03°09'N, 59°16'W, 26 Oct. 1991, *B. Hoffman 409* (CAY, US); Marudi Mt., 0.5 km NE of mine compound, 400 m, 02°14'N, 59°10'W, 11 Sep. 1993, *T.W. Henkel 2831* (NY, US); Tautowan Mt., base & slope, 10 km E of Dadanawa Ranch Compound, 260 m, 02°49'N, 59°25'W, 4 Jun. 1997, *D. Clarke 5145* (US); Wassari Mts., 275-400 m, 01°33'54"N, 059°14'18"W, 4 Sep. 1999, *D. Clarke 8219* (NY, US).

HAITI. **L'Artibonite**. Vicinity of Kalacroix, Section Dessalines, 700 m, 11 Dec. 1925, *E.C. Leonard 7810* (US); Vicinity of Ennery, 20 Jan. 1926, *E.C. Leonard 9042* (NY, US); **Nord**. Vicinity of Plaisance, 28 Jun. 1920, *E.C. Leonard 9352* (BM); Vard, Bayeux, N. Brigand at Thiband, 24 Nov. 1924, *E.L. Ekman 2624* (G, K, US); Massif du Nord, slope of M. Palombal, 700 m, 19 Jun. 1925, *E.L. Ekman 4330* (US); Vicinity of St. Michel d'Atalaye, 350 m, 18 Nov. 1925, *E.C. Leonard 7158* (BM, US); Vicinity of St. Michel de l'Atalaye, 7 Dec. 1925, *E.C. Leonard 7776* (NY, US); Vicinity of St. Michel de l'Atalaye, 350 m, 26 Dec. 1925, *E.C. Leonard 8475* (US);Vicinity of Plaisance, 27 Jan. 1926, *E.C. Leonard 9282* (US); Vicinity of Pilate, 325 m, 10 Feb. 1926, *E.C. Leonard 9668* (P, US); Vicinity of St. Louis du Nord, 30 Mar.-7 Apr. 1929, *E.C. Leonard & G.M. Leonard 14197* (NY, US); La Victoire, 3 Oct. 1943, *L.R. Holdridge 1738* (BM, NY, US); **Ouest**. Vicinity of Mission, Fonds Varette, 1000 m, 18 Apr. 1920, *E.C. Leonard 3670* (BM, NY, US); Vicinity of Furcy, 1300 m, 5 Jun. 1920, *E.C. Leonard 11563* (US); Massif de La Selle, Port au Prince, Morne de L'Hôpital, 750 m, 21 Oct. 1924, *E.L. Ekman 2224* (US); Vicinity of Mission, Fonds Varettes, 1000 m, 29 Apr. 1920, *E.C. Leonard 3976* (US); Miragoane and vicinity, 20 Sep. 1927, *W.J. Eyerdam 594* (NY, US).

HONDURAS. **Atlantida**. 17 km SSE of La Ceiba along Río Cangregal, 26 Jun. 1970, *G. Davidse & R.W. Pohl 2197* (MO, NY, US); Jutiapa, 36 km E de La Ceiba, Corozales, 13-18 Apr. 1976, *C. Nelson & al. 3436* (MO); **Cortés**. Montaña La Cumbre, 21 Mar. 1962, *A. Molina 10566* (US); **Gracias a Dios**. Camp Tiro, 2 miles NW of Bulebar, on third northern branch of Quebrada Tiro, tributary of Río Platano, 15°43'N, 84°50'W, 4 Apr. 1981, *J. Saunders 1216* (MO); **Olancho**. Along Río Olancho, on road between San Esteban and Bonito Oriental, 3.3 miles SW of border with Colón Department, along Río Grande, 20.8 miles SW of junction in Highway to La Ceiba and Trujillo, vicinity of Bonito Oriental, 350-400 m, 15°31'N, 85°42'W, 8 Feb. 1987, *T.B. Croat & D.P. Hannon 64486* (MO).

JAMAICA. Clarendon. Richmond Hill, Nov. 1900, *C.F. Millspaugh 1968* (US); Peckham Woods, 27 Dec. 1912, *W. Harris 12768* (US); Upper west slope of Crofts Mountain, 2250-2500 ft, 4 Oct. 1968, *G.R. Proctor 29244* (US); Clarendon, at top of N side Round Hill near Milk River, 300 m, 29 Dec. 1980, *V. Kapos 1606* (MO). **Manchester**. New Forest, Southern Manchester, 8 Nov. 1912, *A.S. Hitchcock 9893* (US); NW of Mandeville, Dec. 1956, *G.R. Proctor 16025* (BM); **Middlesex**. Shaw Park, Ocho Ríos, 13 Jan. 1948, *F.W. Hunnewell 18805* (NY); **St. Andrew**. Newcastle, 30 Sep. 1912, *A.S. Hitchcock 9335* (US); Gordontown, 6 Oct. 1912, *A.S. Hitchcock 9380, 9382* (US); Hills back of Barican, Ram's Horn Range, 19 Oct. 1912, *A.S. Hitchcock 9569, 9570, 9571* (US); North slope of Catherines Peak, 29 Oct. 1912, *A.S. Hitchcock 593* (BM, C, G, K, L, MO, NY, P, US, W); New Castle, 3 Nov. 1912, *W. Harris 11398* (BM, C, K, MO, NY); Salt Hill, 3 Nov. 1912, *W. Harris 11410* (BM, K, US); Hope Grounds, 11 Nov. 1912, *W. Harris 11405* (C, K, NY); Blue Mts., Robertsfield, 3 Dec. 1912, *W. Harris 11491* (NY); Mt. Diablo, Feb. 1916, *H.N. Ridley 24* (BM, US); Mt. Lebanon, 4 Jan. 1917, *W. Harris 12488* (BM, K, MO, NY, US); Mt. Charles Distr. below Mavis Bank, 1800 ft, 14 Dec. 1954, *G.R. Proctor 9626* (NY, US); Road to Bellevue, 17 Nov. 1957, *T.G. Yuncker 17407* (BM, G, MO, NY); Hopewell, below Red Light, 10 Dec. 1957, *A.D. Skelding 3481* (NY); Greenwich Bridle Path, 28 Feb. 1960, *C.D. Adams 6399* (BM); Silver Hill, 3000 ft, secondary growth or mountainside, 24 Nov. 1971, *G. Davidse & G. Proctor 3247* (MO, US), **n = 18!** (Davidse 1978); Along road just above Gordon Town, 24 Nov. 1971, *G. Davidse & G.R. Proctor 3250* (K, MO, NY, US), **n = 18!** (Davidse 1978); **St. Ann**. Near Faith's Pen, 14 Jan. 1958, *R.A. Howard & G.R. Proctor 14990* (BM); James Webster Patent, 24 Nov. 1972, *G.R. Proctor 33008* (BM, US); **St. Catherine**. Ewarton to Linstead, 9-11 Oct. 1912, *A.S. Hitchcock 9409* (US); Ellis Mountain, Caymanas, Dec. 1954, *G.F. Asprey 2222* (NY); 4 miles S of Ewarton near Riverhead, 1200 ft, 12 Feb. 1961, *C.D. Adams 8946* (MO); **St. James**. Near Montego Bay, Mar. 1916, *H.N. Ridley 34* (BM, US); Flamstead, 26 Nov. 1917, *W. Harris 11469* (BM, K, NY); The Cockpit Country, near Flagstaff, 23 Dec. 1961, *C.L. Lundell 16983* (MO); **St. Thomas**. 1-13 1909, *N.L. Britton 4045* (NY); Vicinity of Creighton Hall, east side of Yallahs Hill, 500 ft, 24 Nov. 1963, *G.R. Proctor 24243* (US); 2.4 miles SE of Cedar Valley along road to Saeforth, 350 m, 25 Nov. 1971, *G. Davidse & E. Convoy 3266* (MO); **Trelaway**. Troy, 6 Nov. 1912, *A.S. Hitchcock 9808, 9813* (US); Troy, 19 Oct. 1917, *W. Harris 12650* (K, MO, NY, US); Burnt Hill Between Albert Town and Troy, 560 m, 1 Feb. 1980, *A. Gentry & V. Kapos 28320* (MO, NY).

LEEWARD ISLANDS. **Antigua**. Hills above Blubber Valley, 4-16 Feb. 1913, *J.N. Rose & al. 3484* (NY, US); Antigua, 200-850 ft, 15 Oct. 1931, *H.E. Box 115* (BM, K, MO, US); **Guadeloupe**. s.d., *C. Bertero s.n.* (FI-Webb, TO); Gourbeyre, 1893, *P. Duss 3182* (NY); Morne Boucanier, 10 Feb. 1895, *P. Duss 3613* (US); Forêt dense, bois traces, Malanga, 2 Jan. 1937, *H. Stehle 1945* (US); Basse Terre, route menat a' la crete de village, 500 m, 10 Apr. 1974, *C.H.L. Sastre & F. Sastre 2539* (MO); Basse-Terre, Côte sous le Vant, Crête de Village, 500 m, 11 Nov. 1976, *C.H.L. Sastre & al. 4258* (P); Grands Fonds de Saint-Anne, 18 Dec. 1987, *Fournet 4272* (P); Petit Bourg, Montebello, 16 Apr. 1989, *Fournet 4482* (P); Pigeon (Bouillante), sous-bois de forét littorale remaniée, 28 Jan. 2004, *P. Bamps s.n.* (BR); **St. Croix**. Christiansted, 20-24 Feb. 1913, *J.N. Rose & al. 3624* (NY); **St. Kitts**. 13 Oct. 1919, *A.S. Hitchcock 16353* (US); St. Kitts, 28 Jan. 1932, *H.E. Box 160* (BM, K, MO, NY, US).

MEXICO. **Baja California**. Cañon del Caduco, E base of Cerro de la Giganta, Sierra de la Giganta, 7 Oct. 1951, *A. Carter & L. Kellogg 3110* (K, US); **Chiapas**. Near the junction of the Río Perlas and Río Jataté at San Quintin and near Laguna Miramar, 18 Mar. 1955, *E.R. Sohns 1617* (K, US); Sierra Madre, 3 Nov. 1960, *T. Tateoka 1002* (K); Ixtapa, 7 Feb. 1981, *J. Bauml & al. 586 B* (US); Chichoasén, 8 Nov. 1988, *A. Reyes García & Urquijo 1147* (BM); Chiapas, Ocosingo, al NO de Nuevo Guerrero, sobre el arroyo a 1 km del poblado, 193 m, 16°59'23"N, 91°17'27"W, 6 Jul. 2002, *D. Aguilar M. 1719* (MO); Villa Corzo, La Cascada, Nuevo Refugio, 15°59'32"N, 93°26'50"W, 1 Aug. 2003, *E.M. López 3072* (MO); **Morelos**. Salto de San Anton prope Cuernavaea, 19 Jan. 1926, *G.J.N. Woronow 2460* (K); **Oaxaca**. Canyon of the Río Zavaleta near the village of San Pablo Quatro Venados, 15-18 km WSW of Oaxaca, 20-25 Jan. 1937, *W.H. Camp 2461* (NY); 1,5 miles E of Ayautla on road to Tuxtepec, 31 Jan. 1981, *J. Bauml & M. Kimnach 464* (US); Choapam, Yaveo, trail to San Juanito, 1

Apr. 1938, *Y. Mexia 9252* (G, K, MO, NY, US); Oaxaca, San Carlos Yautepec, 6.4 km al SE del Camarón carretera a Tehuantepec. 1075 m, 20 Sep. 1988, *R. Torres C. 12581* (MO); Istmo de Tehuantepec, Juchitán de Zaragoza, La Ventosa, 42 m, 16°34'03"N 94° 57'04"W, 24 Oct. 2013, *F. Sánchez 170* (US); **Tabasco**. 12 km E of Tacotalpa toward Tapijulapa, 9 Mar. 1980, *C. Cowan 2796* (MO, NY); **Veracruz**. Colipa, Mar. 1841, *F.M. Liebmann 289* (C), *290* (K); Barranca de Jenampa, Zacuapan, Jan. 1912, *C.A. Purpus 6206* (BM, MO, NY, US); Cerro San Cristóbal, frente a Orizaba, 17 Dec. 1970, *A. Lot 1102* (US).

NICARAGUA. **Boaco**. Hacienda San Louis, ca 18 km al N de Camoapa, 400 m, 12°34'N, 85°30W, 27 Dec. 1984, *D. Soza & al. 295* (MO); **Carazo**. Jinotepe, 3-7 Dec. 1911, *A.S. Hitchcock 8674, 8695* (NY, US); Jinotepe, Wiwili, Comunidad Boca de Plis, Reserva Bosawas, Territorio Misquito Indian Tasbaika Kun, parcela 1, Finca de Natividad Urbina, 500 m al S, 200-300 m, 7 Feb. 2008, *E.M. Urbina 253* (MO); **Chontales**. Near Santo Domingo, 9 Apr. 1961, *G.S. Bunting & L. Licht 1167* (NY); **Jinotega**. along Lago Apanás, 4 Dec. 1973, *L.O. Williams & A. Molina 42756* (NY); Road between Río Bizcocho and Río El Jordan, 350-550 m, 12°16'N, 85°17'W, 18 Dec. 1983, *W.D. Stevens 22598* (K, MO); Bocay, Reserva Natural Kilambé, Comunidad San Miguel de Kilambé, 700-900 m, 13°31'N, 85°37'W, 6 Jan. 2001, *R. Rueda & al. 15294* (MO); **Matagalpa**. Cut-over hills about 15 km NE of Matagalpa along Río Las Cañas, 14 Jan. 1965, *L.O. Williams & al. 27506* (MO, NY, US); Chontales, Santo Domingo, 13 Jan. 1970, *E. Narvaez 3356* (BM, MO, NY); Matagalpa, Wet Montane Cloud Forest area, Finca Santa Maria de Osyuma, Cordillera Central de Nicaragua, 30 Nov.-4 Dec. 1973, *L.O. Williams & A. Molina 42666* (NY); Matagalpa, Finca La Castilla, 20 km NE de la ciudad de Matagalpa, camino de entrada, 500-550 m, 13°01'N, 85°47'W, 22 Jan. 1982, *D. Castro 2420* (MO); **Río San Juan**. 2 km NW of Sábalos, 23 Feb. 1984, *P.P. Moreno 23302* (BM); Río San Juan, El Castillo, comunidad Che Guevara, 60 m, 11°03'33"N, 84°22'33"W, 8 Apr. 2005, *L. López 547* (MO); **San Juan**. San Juan de Nicaragua, 1841, *Friedrichstahl 549* (W); **Zelaya**. Vicinity of Wani including Río Uli, 90-110 m, 13°41'N, 84°50'W, 15 Mar. 1978, *W.D. Stevens & al. 7214* (MO); Zelaya, Río Punta Gorda, al E de la Comarca del Salto del León, camino al caserio hacia la Gloria, 11°31'N, 84°20'W, 23 Feb. 1994, *R. Rueda & al. 3355* (MO).

PANAMA. **Bocas del Toro**. Vicinity of Chiriquí Lagoon, 19 Feb. 1940, *H. von Wedel 1856* (MO, US); 1 km NW of Bocatorito on SE side on island, 9 Feb. 1989, *P.M. Peterson & C.R. Annable 6722* (MO); Approximately 3.5 km S of Tiger Key on the mainland, 0-100 m, 20 Feb. 1989, *P.M. Peterson & C.R. Annable 6940* (MO); 5 km S of Tiger Key on the mainland near Cacao Boquete just N of Ensenada de Boquete, 5-110 m, 24 Feb. 1989, *P.M. Peterson & C.R. Annable 7072* (MO); Carretera Fortuna-Chiriquí Grande, 8°50'49"N, 82°10'59"W, 129 m, 21 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 860, 861, 862* (FT, PMA, SCZ); **Chiriquí**. Rabo de Puerco, 8 km W of Puerto Armuelles, 50-150 m, 18 Feb. 1973, *T.B. Croat 21968* (L, MO); Quebrada Quanabanito beyond La Represa 2 miles SW of Puerto Armuelles, 0-200 m, 20 Feb. 1973, *T.B. Croat 22050* (K, MO, NY); Cañas das Gordas near Costa Rica Border on road to Volcano, 800-1200 m, 26 Feb. 1973, *R. Liesner 267* (K, MO, NY, US); Guanabano, along Quebrada Guanabano, 0-100 m, 3 Mar. 1973, *T.B. Croat 22513* (MO, US); 17 km NE of San Felix on new road to Cerro Colorado copper mines, 1000 m, 18-19 Mar. 1974, *M. Nee 10759* (MO, PMA); Along road from Puerto Armuelles to San Bartolo Limite, 7 miles W of Puerto Armuelles, 120 m, 19 May 1976, *T.B. Croat 36016* (MO); Santa Marta, Bugaba, 3 Dec. 1995, *A. Arauz 103* (PMA); **Chorrera**. Río de Jesus, Los Diaz, muy cercano a Los Catillos, 24 Feb 2012, *O.O. Ortiz & al. 516, 519* (PMA); **Coclé**. Valley of the upper Río Mata Ahogado, 350 m, 31 Dec. 1936, *P.H. Allen 142* (MO, US); Coclé, road from La pintada to Coclesito, ca. 600 m, 8°45'N, 80°30'W, 7 Feb. 1983, *C. Hamilton & G. Davidse 2835* (BM, MO); Coclé, Valle de Antón, 2 km del pueblo, 8°81'35"N, 80°06'51"W, 625 m, 16 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 828* (FT, SCZ); **Colón**. Between France Field and Catival, 9 Jan. 1924, *P.C. Standley 30153* (US); Colón, Río Viejo, vicinity of Puerto Pilón, 2 Feb. 1947, *P.H. Allen 4102* (G, NY, US); Camino a la zona maderera de Santa Rita, 28 Mar. 1968, *M.D. Correa & R.L. Dressler 885* (MO, PMA); Nombre de Dios y San Antonio, 7 Feb. 1996, *C. Guerra & A. Espinosa 595* (FT, PMA); Carretera Portobelo-Nombres de Dios, 9°33'33"N, 79°34"33'W, 40 m, 29 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 919* (FT, SCZ); **Darién**. Río Pinas, 2 Mar. 1967, *J.A. Duke 10569* (MO); Forest near Yaviza, sea level, 8 Jan. 1975, *A. Gentry 13488* (MO, PMA); Ensenada del Guayabo, 10 Jan. 1983, *N. Garwood & al. 81* (BM); **Herrera**. 27 Aug. 1961, *J.E. Ebinger 1067* (US); Disturbed area surrounding Chepo de Las Minas, 700 m, 19 Dec. 1977, *J.P. Folsom & al. 7044* (MO); Herrera, road to 8 miles SW of Las Minas, 4 Nov. 1979, *W.G. D'Arcy & T. Antonio 13493* (MO); Herrera, 3-7 km W of Las Minas on road to El Toro, 200-600 m, 23 Jan. 1981, *K. Systma & W.G. D'Arcy 3188* (MO); **Panamá.** Canal Zone, 1850, *A. Fendler 371* (K, MO, US); Canal Zone, Río Grande, near Culebra, Dec. 1910, *H. Pittier 2118* (NY, US); Canal Zone, between Miraflores and Corozal, Jan. 1911, *H. Pittier 2196* (BM, NY, US); Canal Zone, Gatún Lake, 15 Dec. 1911, *A.S. Hitchcock 416* (BM, C, K, L, MO, NY, P, US, W), *417* (BM, C, G, K, L, MO, NY, US, W); Camino de Las Sabanca, Nov. 1921, *Bro. Heriberto 257* (NY, US); Gatún, 21 Jan. 1922, *C.H. Ostenfeld s.n.* (US); Canal Zone, Chiva-Chiva Trail, Red Tank to Pueblo Nuevo, 1 Mar. 1923, *C.V. Piper 5219* (US); Canal Zone, Ancon, 25 Feb. 1923, *C.V. Piper 5281* (US); Canal Zone, Cerro Gordo, 5 Dec. 1923, *P.C. Standley 25955* (C, US), *25987* (US); E of the Río Tecumen, 11 Dec. 1923, *P.C. Standley 26651* (C); Canal Zone, Gamboa, 26 Dec. 1923, *P.C. Standley 28320* (C, US); Balboa, Nov. 1923-Jan. 1924, *P.C. Standley 26065* (K, MO, US); Canal Zone, 1924, *F.W. Popenoe 47* (K, NY); Canal Zone, Las Cascadas Plantation, 4 Jan. 1924, *P.C. Standley 29523* (C, US); Panamá, between Matias Hernandez and Juan Diaz, 21 Jan. 1924, *P.C. Standley 32022* (US); Barro Colorado Island in Gatún, 18-24 Nov. 1924, *P.C. Standley 40837* (US); San José Island Perlas Archipelago, Gulf of Panamá (about 55 miles SSE of Balboa): Barro Colorado Island, 4 Dec. 1931, *O.E. Shattuck 528* (MO, P, STRI); Canal Zone, Las Cruces Trail, 25 Feb. 1935, *A.A. Hunter & P.H. Allen 760* (MO, US); Met Road, erect, bambolo-like, 6 ft. tall, stems several, roadside, 8 Jan. 1946, *I.M. Johnston 1078* (BM, FI, P, US); Valley in Area 11B, scrambling in ticket near open springy place, 28 Jan. 1946, *I.M. Johnston 1272* (FI, US); Canal Zone, vicinity of Río Cocoli, Road K-9, 31 May 1959, *W.L. Stern & al. 342* (MO); Canal Zone, 11 miles NE of Balboa, Finca Bergeron, 19 Feb. 1962, *W.J. Eyerdam 12079* (US); Canal Zone, Fort Clayton, 1 mi E Tocumen airport on side road off of Inter-Amer Highway, 19 Dec. 1965, *K.E. Blum & E. Tyson 1962* (MO, SCZ); Los Santos, 12 miles S Macaracas, 22 Jan. 1966, *E.L. Tyson & al. 3078* (MO); Canal Zone, Chiva Chiva Trail near Miraflores Lake, 19 May 1966, *J.D. Dwyer & K. Blum 4011* (MO, US); Canal Zone, Hill opposite Paraiso, 29 Nov. 1966, *J.D. Dwyer 7150* (MO, NY); Pacora-Chepo Highway, vicinity of Pacora River, 7 Dec. 1966, *S. McDaniel 8178* (MO); Barro Colorado Island, clearing at end of Harvard Trail, common, 12 Dec. 1967, *T.B. Croat*

4259 (MO, SCZ, STRI); Barro Colorado Island, 15 Apr. 1968, *T.B. Croat 4821* (MO); Barro Colorado, Burrunga Pt., 17 Feb. 1969, *T.B. Croat 8009* (MO, SCZ, STRI); Canal Zone, forest near Summit Golf Club, 13 Dec. 1970, *T.B. Croat 12791* (MO, SCZ); Panamá, Route T3, N of Buenas Aires, 27 Dec. 1970, *T.B. Croat 12924* (MO, NY, SCZ); Canal Zone, Barro Colorado island, Burrunga Point Clearing, 29 Dec. 1970, *T.B. Croat 12942* (MO); Bejuco, Los Pozos-Chame, 28 Nov. 1972, *M. Troetsch 22* (MO); Panamá, Río Tapia, Dec. 1923-Jan. 1924, *P.C. Standley 28142* (K) 3 km S of Alcade Diaz, 440 m, 18 Dec. 1973, *M. Nee 8857* (K, MO, NY); Canal Zone, junction of Chiva-Chiva and Gaillard Highway, shores of Gatun Lake, 50 m, 9°00'N, 79°37'W, 26 Apr. 1982, *S. Knapp & R. Schmalzel 4869* (MO); Panamá, Cerro Cabra, small cut over hill just W of Canal Zone on the coast Veracruz, 1000 ft, 30 May 1978, *B. Hammel 3275* (MO); Panamá, Cerro Galera, just W of Tharcher Bridge, 100 m, 8°55'N, 79°35'W, 15 Feb. 1983, *C. Hamilton & Y. Palmer 2956* (MO); Barro Colorado Island, East shoreline of Fairchild Peninsula, 22 Mar. 1986, *N. Garwood 1741 A* (BM, PMA); Barro Colorado Island, near heliport, 3 Mar. 1988, *N. Garwood 2282 A* (PMA); Gamboa, area de rostrojo despues del puente sobre el Río Chargres, en direcion a Gamboa, 9°06'49"N, 79°41'51"W, 49 m, 27 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 917, 918* (FT, PMA, SCZ); **San Blas**. Soskatupu, island ca. 1.5 miles long, 0.5-0.7 miles broad, 0-150 m, 15 Aug. 1967, *T.S. Elias 1667A* (MO); Beginning of El Llano-Carti-Tupile road, 200-500 m, 8 Jan. 1974, *J.D. Dwyer & M. Nee 11994* (K, MO, US); Río Cangandí, 9°24'N, 79°24'W, 50-100 m, 18 Feb. 1985, *G. de Nevers 4927* (MO, PMA); **Veraguas**. Trail between Cañazas and the foot of the Cordillera Central, headwaters of Río Cañazas, 300-600 m, 8 Feb. 1937, *P.H. Allen 176* (MO, US); On Caribbean slope above Río Primero Brazo 5 miles NW of Santa Fe, 700-1200 m, 18-19 Mar. 1973, *T.B. Croat 23187* (K, MO, NY, US); Río Santa Maria along road to Santiago, 5 km S of Santa Fé, 250-300 m, 18 Nov. 1973, *M. Nee 8136* (L, MO, PMA); Open weedy roadside and open to brushy "savanna" pasture, 2 km NW of Atalaya, 19 Nov. 1973, *M. Nee 8201* (NY, PMA); Lower Montane Wet Forest, 6-7 km W of Santa Fé, 17 Feb. 1974, *M. Nee 9836* (MO, NY, PMA); Soná, Bahía Honda, Lerén, 30 Jan. 2002, *A. Ibáñez & al. 1516* (MA); Santa Fé, Alto de Piedra, Carretera Alto de Piedra-El Guabal, 8°31'38"N, 81°07'51"W, 617 m, 18 Jan 2012, *M.N.S. Stapf & R.M. Baldini 844* (FT, SCZ).

PARAGUAY. Alto Paraná. In regione fluminis Alto Paraná, 1909/10, *K. Fiebrig 6014* (G, K, US); Cerro Barrero, circa Fuente Olimpo, 28 Mar. 1980, *L. Bernardi 20372* (G, MO); Reserva Biologico Limoy de Itaipu Binacional, 24°51'S, 54°33'W, 18 Apr. 1986, *D.R. Brunner & S. Caballero 1850* (G, MO); Pto. Bertoni, 31 Mar. 1993, *A. Schinini & al. 28255* (G); Alto Paraná, Reserva Biologica Limoy, 10 Feb. 1997, *M. Dematteis & al. 559* (G); 95 km W of Ciudad del Oeste, km 235-238 near San Marcos, 25°24'S, 55°30'W, 17 Mar. 1999, *J.R. Grant & J.R. Rundell 3283* (US); Itaipu Binacional Paraguay-Brazil, Tati Yupi Biological Refuge, 220 m, 25°21'18"S, 54°37'54"W, 19 Jul. 2003, *E.M. Zardini & al. 60202* (MO); **Amambay**. Inter Río Apa & Río Aquidaban, San Luis, 1908-09, *K. Fiebrig 4710* (BM, G, K, L); Cerro Corá, collina circa Colonia Aceite, 13 Apr. 1980, *L. Bernardi 20561* (G, MO); Parque Nacional Cerro Corá, base del Cerro Muralla, 7 Feb. 1982, *J. Fernandez Casas & J. Molero 6039* (G, MO, NY); Parque Nacional Cerro Corá, 300 m, 22°39'S, 56°03'W, 11 Feb. 1982, *J.C. Solomon & al. 6863* (MO); Ruta 3, Arroto Negla., 16 Dec. 1983, *R. Vanni & al. 339* (G, MO); Parque Nacional Cerro Corá, Remonta Cué, 2240'S, 5605'W, 2 May 1992, *O. Morrone & J. Pensiero 542* (MO); Parque Nacional Cerro Corá, Cerro Muralla, 250 m, 22°39'S, 55°59W, 7 May 2001, *F.O. Zuloaga & O. Morrone 7310* (MO); **Boquerón**. Gran Chaco, ad ripam occidentalem flum. Paraguay, 5 Oct. 1905, *E. Hassler 2868* (BM, G, K); Puerto Casado & vicinity, Cerro Galvan, 23 Oct. 1956, *T.M. Pedersen 4155* (C); **Caaguazú**. In vicinity Caaguazú, Mar. 1905, *E. Hassler 9143* (BM, G, K, NY, W); **Caazapá**. Estancia Golondrina, Reserva Privada Ypeti, 2532'20"S, 5529'01"W, 22 Jul. 1998, *E.M. Zardini & G. Hellman 48926* (MO); **Canindeyú**. Canindeyú, camino Jejui-mi-Lagunita, km 8, 17 Apr. 1996, *G. Marín 146* (BM, MO); Jejui-mí, 14 Aug. 1996, *B. Jiménez & G. Marín 1379* (BM, MO); **Chaco**. Cerro Leòn, del piede del Cerro hasta lomada al S de la meseta central, 16 May 1985, *A. Charpin & L. Ramella AC 21656* (G); S. Cruz, Cerro San Miguel, Fortin Raselo, 6 Mar. 1989, *F. Mereles & L. Ramella 2717* (G), *2804* (G); **Central Paraguay**. Central, in regione lacus Ypacaray, May 1913, *E. Hassler 12514* (G, K, L, MO, NY); Near Asuncion, 1888-90, *T. Morong 755* (G, K, MO, NY), *641* (G, K, MO, NY, US), *780* (NY); Central Paraguay, 15 Feb. 1874, *B. Balansa 40* (BM, G, K, L, US); Santa Barbara prés di Villa-Rica, 27 Feb. 1876, *B. Balansa 41* (L, P); Asunción, Colonia Elisa, Jul. 1893, *C.A.M. Lindman 1701* (UPS, US); Cordillera de Altos, 1898-1900, *E. Hassler 3731* (G, K, NY); Dep. Central, Villa Elisa, 12 Apr. 1961, *T. Pedersen 5899* (C, K, US); Asunción, Jardín Botánico, 5 May 1972, *A. Schinini 4728* (G, K, MO); Central, Tarumandy, 2 Apr. 1973, *A. Schinini 6200* (G); Central, 2.5 km W from entrance to Tavavory, 25°30'S, 57°30'W, 18 May 1992, *E. Zardini & T. Tilleria 31734* (MO); **Concepción**. 8-10 km al sur de l'Arroto Tagatiya-mi, 170 m, 22°42'S, 57°30'W, 5 Apr. 1986, *D.R. Brunner 1775* (G, MO); **Cordillera**. Caacupé, 11 Apr. 1950, *A. Burkart 18338* (MO, US); Serrania Tobatí, Meseta Ybitù Silla, 297 m, 25°12'S, 57°07'W, 25 Aug. 1988, *E. Zardini 6693* (MO); W side of Rio Piribebuy basin, 27 km W of Arroyos y Esteros, 25°08'S, 57°18'W, 19 May 1990, *E. Zardini & C. Velázquez 20302* (MO); Cordillera, 5 km SE of Emboscada on road to Nueva Colombia, 25°08'S, 57°15'W, 9 Jun. 1990, *E. Zardini & E. Velázquez 21062* (BM, K, MO), *21155*, *21212*, *21255* (MO); Cordillera de Ybytyruzú, Melgarejo-Cerro Arati, 25°46'S, 56°16'W, 10 Jul. 1992, *E. Zardini & P. Aquino 32624* (K, MO); **Guairá**. Parque Nacional 7 Quedas, 24 Mar. 1977, *G. Hatschbach 39811* (G, NY); Colonia Independencia, 25°40'S, 56°15'W, 15 Apr. 1984, *W. Hahn 2250* (L, MO, NY); Cordillera de Ybytyruzú, Cerro Peró, 1 km W of Destacamento Torero, 25°55'S, 56°15'W, 17 Feb. 1989, *E. Zardini & C. Velázquez 10912* (BM, MO); Cordillera de Ybytyruzú, road Melgarejo-Antena, 5 km S of Melgarejo, 25°55'S, 56°15'W, 13 Mar. 1989, *E. Zardini & R. Velázquez 11455* (MO); Road Melgarejo-Antena, 25°55'S, 56°15'W, 5 Mar. 1989, *E. Zardini & C. Velázquez 11274* (K, MO), *11313* (MO); Col. Independencia, Ayo. Guazù, camino a San Gervasio, 27 Mar. 1993, *A. Schinini & al. 28045* (G), *28066* (G); **Paraguarí**. Yguarón, Cerro Curupayty, 5 May 1975, *P. Arenas 1197* (K); Parque Nacional Ybycui, 26°40'S, 55°10'W, 20 Apr. 1984, *W. Hahn 2302* (L, MO); Parque Nacional Ybycui, cuenca del Arroyo Minas, 26°05'S, 56°51'W, 15 Jun. 1985, *D.R. Brunner & L. Pérez 1200* (G, MO); Costa Segunda Cerro Palarios, 250 m, 25°25'S, 57°10'W, 31 May 1988, *I. Basualdo & al. 1551* (MA, MO); Cerro Palacios, 250 m, 25°25'S, 57°10'W, 3 Aug. 1988, *E. Zardini 6357* (MO); Arroyo Corrientes, National Park Ybycuti, 26°00'S, 56°46'W, 10 Feb. 1993, *E. Zardini & Guerrero 34980* (K, MO); **Presidente Hayes**. Villa Hayes, Estancia La Golondrina, 24°55'S, 57°40'W, 9 Sep. 1982, *W. Hahn 699* (L, MO); **San Pedro**. Primavera, Alto Paraguay, 24 Feb. 1956 *A.L. Woolston G. 87* (C, K, NY, US), 28 May 1956 *A.L. Woolston G146* (C, NY); Calle ovetense, 12 km al NE de Choré, 3 Oct. 1987, *E. Zardini & C. Benítez*

3399 (MO); Yaguareté forest, trail to Rio Aguaray, 23°46'16"S, 55°59'37"W, 20 Jun. 1995, *E. Zardini & C. Balbuena 42937* (MO); Yaguareté forest, Northern boundary, 23°46'49"S, 56°11'49"W, 27 May 1997, *E.M. Zardini & S. Zavala 46707* (MO).

PERÚ. **Amazonas**. Bagua, valley of Río Marañón above Cascadas de Mayasi near Campamento Tte. Montenegro, 450 m, 3-4 Sep. 1962, *J.J. Wurdack 1806* (K, US); Quebrada Huampami, Río Cenepa, Chacra, 15 May 1973, *R. Kayap 744* (US); Quebrada Chichijam, Río Cenepa, 920 ft, 7 Jun. 1973, *E. Ancuash 562* (MO, NY, US); Río Cenepa, 24 May 1973, *G. Davidse 452* (K); Quebrada Satik, 16 Jul. 1974, *R. Kayap 1096* (K, MO); Prov. Bongará, Distr. Sipabamba, along Quebrada Fortuna, 1300 m, 5 May 1981, *K. Young & M. Eisenberg 333* (MO); Luya, Camporredondo, Fundo Cedro, 2450-2550 m, 24 May 1989, *C. Diaz & al. 3508* (MO); Condorcanquí, Distr. El Cenepa, Region NE del Marañon, Comunidad de Kusu-kubaim, Río Comaina, 700 m, 04°25'S, 78°16'W, 17 Aug. 1994, *R. Vasquez & al. 18830* (MO); Imaza, Kampaensa, NE del Marañon RENOM, 300-350 m, 04°55'S, 78°19'W, 21 Oct. 1995, *V. Quipuscoa S. 316* (MO); Bagua, Aramago-Muyo, 380 m, 5°25'00"S, 79°30'00"W, 6 Nov. 1999, *R. Rojas & al. 739* (MO); **Ayacucho**. Estrella, between Huanta and Río Apurimac, 8-14 May 1929, *E.P. Killip & A.C. Smith 30674* (NY); **Cajamarca**. 2-8 km E of Chirinos, disturbed former *Podocarpus* forest, 1800 m, 05°25 S, 78°52 W, 3 Feb. 1988, *A. Gentry & al. 61089* (MO); San Ignacio, Portachuelo, 1000-1500 m, 05°08'S, 78°57'W, 28 Jan. 1996, *J. Campos & O. Diaz 2233* (MO); San Ignacio, Namballe, entre Pacashal y Las Abejas, 850-950 m, 04°58'00"S, 079°20'00"W, 9 Jul. 1997, *J. Campos & al. 4105* (MO); Cutervo, 5 km N of Santo Domingo de la Capilla on road towards Chiple, 1400 m, 22 Mar. 2000, *P.M. Peterson 15034* (US); Jaen, 11 km W of Highway 5N up Río Tabaconas and 4 km E of Tamborillo, 29 Mar. 2000, *P.M. Peterson & N. Refulio Rodriguez 15096* (K, MO); **Cuczo**. Quispicanchi, Camanti, Maniri, 8 km W de Quincemil, en el camino hacia la represa de la quebrada Yanamayo, 720 m, 13°17'S, 70°48'W, 22 Jul. 1990, *M. Timaná & H. Astete 705* (MO); La Convencion, Distr. Huayopata, San Luis, 1047-3200 m, 12°53'S, 72°44'W, 11 Apr. 2003, *W. Galiano & al. 4864* (MO); La Convencion, Vilcabamba, Chiwanquiri, 881 m, 12°45'16"S, 73°08'06"W, 18 Jul. 2004, *W. Galiano & al. 6620* (MO); **Huanuco**. Churubamba, 1700 m, 24 Sep. 1936, *Y. Mexia 8233* (BM, G, K, MO, NY, US); Huanuco, Tingo Maria, Valley of Río Huallaga, 11-14 Jul. 1937, *C.M. Belshaw 3086* (C); Leoncio Prado, Rupa Rupa, 11 Jun. 1978, *J. Schunke Vigo 10214* (K, MO, NY); Leoncio Prado, road between Tingo Maria and Pucallpá, km 32, 1350 m, 9°10'S, 75°50'W, 3 Jun. 1981, *G. Sullivan & K. Young 1120* (MO, US); **Junín**. Colonia Perené, 23 Oct. 1923, *A.S. Hitchcock 22118* (US); East of Quimirí Bridge, near La Merced, 1-3 Jun. 1929, *E.P. Killip & H.H. Smith 23998* (MA, NY, US); Montayaco, W of San Ramon, 900 m, 27 Jun. 1976, *A. Gentry & G.T. Prance 16430* (MO); N Umgebung von La Merced, Tal des Río Paucartambo, ca. 12 km N Puente Paucartambo, 960 m, 2 Jun. 1979, *H. Teppner 316* (US); De Chanchamayo, La Merced-Puente Paucartambo road, 3 km from La Merced, 720 m, 11°05'S, 75°22'W, 17 May 1983, *D.N. Smith 4050* (MO); **Loreto**. Leticia, Jul. 1902, *E. Ule 6225* (G, K, L)*, 6226* (G, L); Santa Ana, 900 m, 21 Jun. 1915, *O.F. Cook & G.B. Gilbert 1405* (US); Balsapuerto, lower Río Huallaga basin, 150-350 m, 28-30 Aug. 1929, *E.P. Killip & A.C. Smith 28673* (NY, US); Lower Río Huallaga, Oct.-Nov. 1929, *L.O. Williams 4939* (G, US); Quebrada Shanuce above Yurimaguas, 11 Jul. 1972, *T.B. Croat 18083* (MO); Iquitos, trocha de la Astoria hasta el Río Mazan, near the mouth of Río Nanay, 29 May 1973, *S. McDaniel & M. Rimachi 17368* (US); Maynas, Distr. Mazan, Río Amazonas, Varadero de Mazan, 140 m, 19 Aug. 1974, *M. Rimachi 1148* (US); Iquitos, Carretera de Zungaro Cocha, cerca de la quebrada de Shushuna, ca. 150 m, 1 Sep. 1981, *M. Rimachi 5634* (MO); Maynas, Dist. Punchana, Río Nanay, carretera del caseario de Santo Tomas, frente al Puerto de Bellavista, 120-140 m, 17 Aug. 1994, *M. Rimachi 11045* (MO, US); Maynas, Dpto. Punchana, Río Nanay, 2 Nov. 1995, *M. Rimachi 11452* (MO, NY); Prov. de Maynas, zona reservada Güeppí, Frontera con Eciador, por el río Güeppí, arriba de la boca con el río Putumayo, 00°06'01.6"S, 75°10'04.7"W, 213-248 m, 22 Oct. 2007, *N. Dávila & al. 4988* (F); **Madre de Dios**. Parque Nacional Manu, Pakitza, radial 4 a 0.8 km de la trocha Tachigali, 11°56'S, 71°15'W, 23 Apr. 1991, *X. Londoño 613* (US); **Pasco**. Oxapampa, Central Selva, Palcazu Valley, Iscozacin above PEPP Project Camp, 27 Mar. 1986, *J. Salick 7319* (MO, NY); Oxapampa, Distr. Palcazú, San Pedro de Pichanaz, Mirador Pichis, 700-1200 m, 10°30'15"S, 75°04'01"W, 10 Jun. 2004, *R. Rojas & al. 2869* (MO); **San Martín**. San Roque, 1350-1500 m, Jan.-Feb. 1930, *L.O. Williams 7184* (US); Juan Jui, Alto Río Huallaga, 400-800 m, May 1936, *G. Klug 4372* (K, MO, NY, US); Tingo Maria, 625-1100 m, 30 Oct. 1949-19 Feb. 1950, *H.A. Allard 20847* (US); Lamas, Alonso de Alvarado, W de San Juan de Pacayzapa, 800-900 m, 1 May 1973, *J. Schunke Vigo 6138* (MO, NY); Mariscal Cáceres, Fundo Melodía, 800 m, 16 Jul. 1974, *J. Schunke Vigo 7467* (K, MO, US); San Martín, Mariscal Càceres, Distr. Tocache Nuevo, 7 Apr. 1975, *J. Schunke Vigo 8241* (MO, NY); San Martín, Lamas, Alonso de Alvarado, San Juan de Pacaizapa, 1000-1050 m, 29 May 1977, *J. Schunke Vigo 9550* (K, MO, NY); Mariscal Caceres, Distr. Tocache Nuevo, Cerro Sinsin cerca a Bambamarca, 520-700 m, 20 May 1980, *J. Schunke Vigo 11669* (US); Mariscal Caceres, Tocache Nuevo-Juanjui road, 89 km from Tocache Nuevo, 810 m, 0743'S, 7640'W, 23 Jul. 1982, *D. Smith 2145* (MO); Rioja, Distr. Pardo Miguel, entre Paraiso y Perla del Mayo a Aguas Verdes, 1080 m, 05°38'S, 77°36'W, 18 Jun. 1998, *I. Sánchez Vega & al. 9429* (MO); **Tumbes**. Zarumilla, Matapalo, Bosque Nacional de Tumbes, 600-800 m, 19 Dec. 1967, *D.R. Simpson & J. Schunke Vigo 423* (G, NY, US); **Ucayali**. Coronel Portillo, Bosque Nacional de von Humboldt, km 86, Pucalpa-Tingo Maria road, 270 m, 8°40'S, 75°00'W, 8 Aug. 1980, *A. Gentry & M. Horna 29489* (MO).

PUERTO RICO. Porto Rico, 1820, *C. Bertero s.n.* (G); Maricao, 13 Nov. 1884, *P.E.E. Sintenis 215* (G, L) *pro parte*!; Coamo, 13 Nov. 1885, *P.E.E. Sintenis 3062* (G, K, NY, P, US, W); Aybonito, 25 Nov. 1885, *P.E.E. Sintenis 2861* (K, NY, US); two miles NE of Mayagüez, 23 Jan. 1900, *A.A. Heller 4375* (G, L, NY, US); Mount Morales, near Utuado, 15 Mar. 1906, *N.L. Britton & J.F. Cowell 443* (NY); Maricao to Monte Alegrillo, 500-900 m, 3 Apr. 1913, *N.L. Britton & al. 2623* (US); Vicinity of Maricao, 20-23 Oct. 1913, *A. Chase 6218* (US); Vicinity of San Juan, 6 Nov. 1913, *A. Chase 6412* (L); Vicinity of San Juan, 6 Nov. 1913, *A. Chase 6419* (US); Vicinity of Arecibo, 8 Nov. 1913, *A. Chase 6457* (NY); Sierra de Luquillo, 2000-2500 ft, 2 Dec. 1913, *A. Chase 6728* (US); Vicinity of Mayagüez, Monte Mesa, 12 Dec. 1913, *A. Chase 6824* (L), *6809, 6822, 6823, 6825* (US); Vieques Island, Cerra incanta, 28 Jan. 1914, *J.A. Shafer 2570* (NY, US); Along the Guayama, Cayey Road, 5 Mar. 1922, *N.L. Britton & al. 6450* (NY, US); Maricao, 3000 ft, 8 Jan. 1938, *F.H. Sargent 10114* (MO, US); El Dunque-Luquillo, 1 May 1959, *L. Martorell & R. Woodbury 546* (NY); Maricao, 29 Apr.-5 May 1964, *J.A. Duke 7607* (MO); Guavate, Apr. 1968, *R.W. Woodbury s.n.* (NY, US); Cayey, Cerro Avispa, Cercadillo, 10 Feb. 1983, *A.H. Liogier & L.F. Martorell 38886* (NY); Salinas, Barrio Lapa: W peak, Las Tetas de Cayey, 830-840 m 13 Dec. 1986, *G.R. Proctor 42704* (FTG); Canon de San Cristobal Aibonito, 500 m, 23 May 1994, *A.H. Liogier 37301* (MO); Caguas, Bairro Bor-in, 16.9 km N of Guayama, 18°06'N, 66°05'W, 24 Nov. 1994, *D. Atha 827* (NY); Maricao, Maricao Afuera, along Maricao River, 18°10.191'N, 66°59.163'W, 10 Jan. 1995, *P. Acevedo-Rodriguez & J.A. Cedeño 7155* (NY); Maricao, Bairro Maricao Afuera, Río Maricao margins, 18°09'48"N, 66°59'20"W, 23 Dec. 1995, *J.A. Cedeño & H.E. de La Cruz 637* (NY).

SURINAME. Voltzberg, 21 Aug. 1920, *A. Pulle 227* (L); Granitic plateau +/- 8 Km in line from Paka Paka (Saramacca R.) to Ebbatop (v. Asch v. Wijck-Range), 19 Feb. 1951, *J. Florschütz 1563* (C); Circa portum aeronauticum ad flumen Oelemari, 3°6'N, 54°33'W, 1 Apr. 1963, *J.G. Wessels Boer 1158* (C); Lely Mts., 21 Nov. 1975, *J.C. Lindeman & al. 158* (K, NY, P); Lely Mountains, 175 km SSE of Paramaribo, 500-700 m, 13 Oct. 1976, *S. Mori & A. Bolten 8486* (MO, NY); Nickerie, area of Kabalebo Dam Project, roadside near ferry over Kabalebo Road, 30-130 m, 4°-5°N, 57°30'-58°W, 11 Nov. 1980, *J.C. Lindeman & al. 336* (MO, NY, US).

TOBAGO. Tobago, 18-21 Dec. 1912, *A.S. Hitchcock 10270* (US); Tobago, 19 Nov. 1913, *W.E. Broadway 4841* (US); Pigeon Hill, 7 Apr. 1959, *R.S. Cowan 1448* (K, NY); Parlatuvier-Roxborough Trace, Bloody Bay, 8 Apr. 1959, *R.S. Cowan 1484* (K, NY, P, US); Between Studley Park and Hillsborough Dam, 24 Mar. 1993, *Clement & Ryves 270* (BM).

TRINIDAD. Port of Spain, Fort Gorge Road, edge of jungle, 27 Nov. 1912, *A.S. Hitchcock 592* (BM, C, G, K, L, MO, NY, W); St. Anns near Port of Spain, 28 Nov. 1912, *A.S. Hitchcock 594* (BM, C, G, K, L, MO, NY, P, US, W); Chacachare, 4 Dec. 1912, *A.S. Hitchcock 10064* (US); Tabaquite, 10 Dec. 1912, *A.S. Hitchcock 10731* (US); St. Joseph, 17 Dec. 1912, *A.S. Hitchcock 10170* (US); Manzanilla, 29 Dec. 1912, *A.S. Hitchcock 10374* (US); Trinidad, 19 Nov. 1913, *W.E. Broadway 4841* (K); Caparo, 3 Jan. 1915, *W.E. Broadway 4924* (US); St. Francique, Oropuche, 11 Mar. 1915, *W.E. Broadway 4976* (US); St. Ann, 17 Mar. 1920, *N.L. Britton & al. 665* (K, NY); St. Anns Cascade, 4 Dec. 1923, *W.E. Broadway 5170* (G, MO); Aripo Road, 15 Jan. 1926, *W.E. Broadway 5991* (K, US); San Fernando Hill, 18 Jul. 1926, *W.E. Broadway 6397* (US); Maraval, 9 Dec. 1928, *W.E. Broadway 7067* (BM, K, MO, US); Maracas, 26 Jun. 1929, *W.E. Broadway 7233* (BM, G, MO); St. Anns, 21 Feb. 1933, *W.E. Broadway 9064* (BM, G, MO); Port of Spain, hillside along Botanic Garden, 15 Apr. 1933, *T.G. Tutin 412* (US); 1 mile of Arima along eastern main road, 40 m, dense secondary forest, 30 Jul. 1970, *G. Davidse 2446* (MO, US); Northern Range, 4 miles N of the intersection (along the Heights of Guanapo Road) of the Heights of Guanapo Road and Eastern main road (intersection 1 mile E of Arima), 200 m, 30 Jul. 1970, *G. Davidse 2460* (MO); N of Port of Spain along North Coast Road, 420 m, 5 Aug. 1970, *G. Davidse 2561* (MO); Tacarigua Co., trail in forest above St. Benedict's Monastery, trail goes through advanced secondary forest, 1 Jan. 1975, *S.H. Sohmer & S.D. Swanson 9683* (US); Guanaco River 4 miles N de Maturita près Arima, 29 May 1975, *A.M. Raynal 15598* (K).

USA. (**Louisiana**). New Orleans, s.d., *s.coll. s.n.* (Herb. H. van Heurck) (FI-Webb) .

VENEZUELA. **Amazonas**. Orinoco, Lower Orinoco, May 1896, *H.H. Rusby & E.G. Squires 358* (K); 20 km S of Puerto Ayacucho, 2 Nov. 1971, *G. Davidse 2839* (K, MO), **n = 18!** (Davidse 1978); Selva Pintada a mas 20 km de Puerto Ayacucho, 11 Jan. 1978, *J. Bono 184* (FT); Entre la Carretera hacia Samariapo y la pista de aterrizaje del Aereopuerto de Puerto Ayacucho, 75 m, 5°37'N, 67°36'W, 21 Jan. 1980, *O. Huber 4786* (K, MO, NY); **Anzoátegui**. Freites, Burro trail between Sam Durrial and Los Pajariots, 30 airline km ENE of Bergatin and N of Mundo Nuevo, 1200-1400 m, 10°03'N, 64°06'W, 1 Dec. 1981, *G. Davidse & A.C. González 19795* (MO); **Apure**. 42 km NW of Achaguas along Highway to San Fernando de Apure, 110 m, 9 Nov. 1973, *G. Davidse, G. & T. Agostini 3923* (K, MO), **n = 18!** (Davidse 1978); Entre el Samán y el Mantecal, Nov. 1976, *S. Castroviejo & Y. Ginéz López 405* (MA); Páez, Selva de Cutufí, between Cutufí on the Río Cutufí and the Río Sanare, 300-350 m, 7°09-11'N, 71°56-58'W, 8-12 Nov. 1982, *G. Davidse & A.C. González 21834* (MO); **Aragua**. Tovar, 1856-57, *A. Fendler 2494* (K); Near Maracay, El Castaño, 2 Jan. 1942, *H. Pittier 14968* (US); Carretera Las Tejerias-La Tiara, 4 Jan. 1978, *G.S. Bunting 6046* (NY); Aragua, Distr. Ricaurte, 12-18 km al N de la Victoria, hacia la Colonia Tovar, 8 Dec. 1982, *J.A. Steyermark & G. Davidse 127699* (MO, NY); **Bolívar**. Between La Paragua and El Cristo, 290 m, 25 Apr. 1943, *E.P. Killip 37706* (US); E of Miamo Altiplanicie Nuria, 300-500 m, 8 Jan. 1961, *J.A. Steyermark 88188* (K, NY, US); La Gran Sabana, 49 km W of the intersection of the main road to Santa Elena and road to Cabanayen hillsside, 1360 m, 3 Dec. 1973, *G. Davidse 4782* (NY, US); Bolívar, El Pao Viejo, 7 Dec. 1973, *G. Davidse & al. 4968* (K, MO); 2 km E La Paragua, ca. 200 m, 6°56'N, 63°15'W, 23 Jul. 1978, *R. Liesner & A.C. González 5459* (MO, NY); Cedeño, km 103 road Calcara-Puerto Ayacucho, Serrania la Caerbatana, 100-250 m, 07°00'N, 66°30'W, 5 Nov. 1985, *H. van der Werff & B. Holst 7762* (MO); Piar Buen Retiro, 9 km por carretera desde Sabaneta, 330 m, 08°03'00"N, 62°38'00"W, 28 Feb. 1997, *W. Diaz & al. 3134* (MO); 130 m, 5°20'N, 65°45'W, 12 Apr. 1998, *E. Zent & S. Zent 2188* (MO); **Carabobo**. Above Maturin, near Las Trincheras, 21 Dec. 1938, *A.H.G. Alston 5623* (P); Between Maracay and Valencia, south side of Lake Valencia, 4 Mar. 1940, *A. Chase 12339* (K, US); Puerto Cabello, 3 Jan. 1955, *E. Asplund 15118* (NY, UPS); Bejuma, Cordillera de la Costa, N de Bejuma, Palmichal, 10°19'N, 68°14'W, 800-1000 m, 1 Jan. 2010, *W. Meier & N. Flauger 16387* (G); **Districto Federal**. Cerro Naiguatá, 900-1100 m, 2 Nov. 1963, *J.A. Steyermark 91813* (K, US); **Guárico**. San Juan De Los Morros, 29 Nov. 1938, *A.H.G. Alston 5267* (BM); Monagas, Quiriquiri to Caripreto, 29 Apr. 1940, *A. Chase 12580* (US); **Lara**. Around Palmasola, in forest along the Aroa River, 26-28 Jun. 1913, *H. Pittier 6384* (NY, P, US); **Mérida**. Near Barinitas, 70°40'W, 8°45'N, 9 Dec. 1963, *F.J. Breteler 3417* (G, MO, NY, P, UPS); **Miranda**. Petare and vicinity, near Caracas, 800 m, 30 Oct. 1921, *H. Pittier 9893* (US); Las Mostazas on railroad beyond Los Teques, Nov. 1924, *H. Pittier 211* (G); Los Chorros near Caracas, 950 m, 5 Dec. 1938, *A.H.G. Alston 5332* (BM, NY, P, US); Santa Lucia, 150-200 m, 6-8 Mar. 1943, *E.P. Killip & F. Tamayo 37030* (US); Parque Nacional de Guatopo, trail between carretera to summit of Morro de Aguaramal, passing Río Taquasito and Río San Lorenzo, 800 m, 25 Nov. 1961, *J.A. Steyermark 90036* (US, VEN), *90044* (NY, US); **Monagas**. Brushy open slopes of Cerro de la Cueva de Doña Anita, south of and bordering valley of Caripe, 900 m, 7 Apr. 1945, *J.A. Steyermark 61869* (US); N facing mountain slope SW of Caripe, 1030 m, 23 Jun. 1967, *R.A. Russell 9388* (US); **Nueva Esparta**. Isla Margarita, Cerro Copey, 900 m, 19 Mar. 1983, *A.M. Sugden 1123* (K, MO); **Portuguesa**. Distr. Guanare, 17 km NW of Tucupido by road, basin of Represa Tucupido amd lower forested, north slope of Fila Las Palmas, 200-400 m, 69°57'W, 9°01'N, 30 Oct. 1982, *G. Davidse & al. 21470* (MO, US); Portuguesa, W side of Río Guanare, W and a little N of Guanare, 180 m, 9°02'N, 69°47'W, 15 Jan. 1993, *L.R. Phillipe & al. 21252* (MO); **Sucre**. Limite districtos Bermudez-Benitez, Peninsula de Paria, al SE de Carupano, al NE de Maturincito, Cerro La Cerbatana, 700-800 m, 10°37'N, 63°10'30"W, 10 Jan. 2005, *W. Meier & al. 11205* (MO); **Táchira**. Between Las Dantas and Las Adjuntas, 13 km NW of Rubio, 900-1050 m, 7°43'N, 72°25'W, 27 Jul. 1979, *J.A. Steyermark*

& R. Liesner 118776 (MO); 10 km E of La Fundacion, around Represa Dorada, 600-1000 m, 10-13 Mar. 1981, *R. Liesner & A. González 10320* (MO, NY); El Zumbador, hacia Queniquea, 31 Jul. 1984, *J. Bono 4075* (FI); Selva transicional y matorrales, Caserío de Tres Esquinas, arriba de El Valle, aldea Roscio, 1200 m, 5 Jul. 1985, *J. Bono 4987* (FT); **Trujillo**. Selva de Galera a lo largo del Rìo Momboy cerca del Caselìo de Agua Clara, entre Valera y Mendoza, 900-950 m, 12 Jan. 1982, *J. Bono 2694* (FT); Valle del Río Momboy, entre Valera y Mendoza, arriba del Cucharito, hacia La Tapa, 1000-1100 m, 14 Sep. 1988, *J.Bono 6954* (FT); Selva de Galeria y ciénagas a lo largo del Río Momboy, Alrededores de Carmania, subiendo de Valera hacia Mendoza Frìa, 800 m, 7 Apr. 1989, *J. Bono 8111* (FT); **Yaracuy**. Between Marin and Carbonero, 11 Apr. 1922, *H. Pittier 11770* (NY, US); Vicinity of Cristobal Colón, 5 Jan.-22 Feb. 1923, *W.E. Broadway 436* (NY, US), *164, 501, 607, 671, 716* (US), *720* (NY, US), *732* (NY, US); Yaracuy, Distr. San Felipe, Veroes, 5 km S de Bela Vista, 10°23'N, 68°24'W, 11 Jul. 1973, *G. Agostini & al. 1808* (NY); **Zulia**. Carretera El Consejo-Palito Balnco-Sabana de La Plata, en km 6 al SW de El Consejo, 22 Dec. 1977, *G.S. Bunting 6002* (NY); Mara, alrededores del Puesto "El Bosque" de la Guardia Nacional, 1300-1400 m, 10°47'35"N, 72°40'W, 10-15 Nov. 1982, *G.S. Bunting 12242* (MO, NY); Reserva de Burro Negro, 350 m, 10°27'N, 70°49'W, 24 Nov. 1986, *O. Zambrano & L. Alfonso 1406* (MO).

VIRGIN ISLANDS. **St. Croix**. Scenic Drive, W slope of Mt. Eagle, 12 Jan. 1980, *F.R. Fosberg 59223* (BM, FTG, US); **St. John**. Maho Bay, jeep trail to Seiben, 12 Feb. 1988, *P. Acevedo-Rodriguez 2638* (NY); Cruz Bay Quarter, road to Susannaberg, 212 m, 8 Jan. 1991, *P. Acevedo-Rodriguez & A. Siaca 3844* (MO); **Virgin Gorda**. 5 Jan. 1919, *W.C. Fishlock 140* (US).

WINDWARD ISLANDS. **Dominica**. 16 Oct. 1919, *A.S. Hitchcock 16415* (US); Dominica, 20 Jan.–15 Mar. 1933, *G. Proctor Cooper III 26* (US); South Chiltern Estate between Point Michel and Soufrière Bay, 1500 ft, rainforest and citrus plantation, 16 Apr. 1964, *W.R. Ernst 1113* (US); Vicinity of Sophia Bay, 21 Jan. 1966, *K.L. Chambers 2608* (BM, US); St. David near Madjini, 2 Feb. 1969, *R. De Filipps 191* (BM, US); St. Peter, Sindacate Estate, 17 Jan. 1986, *C. Whitefoord 5163* (US); St. David Parish, trail to l'Escalier Tete Chien, Carib Territory, Sineku, 250 m, 27°35'N, 61°15'W, 3 Mar. 1997, *S.R. Hill 28989* (MO); **Grenada**. Grenada, 6 Dec. 1889, *H.F.A. von Eggers 6224* (P, US); Richmond Hill, 1905, *W.E. Broadway 4674* (US); Bequia, 1950, *R.A. Howard 11276* (BM, US); St. Patrick, Marli Hill, 1 Dec. 1957, *G.R. Proctor 17293* (BM, US); **Martinique**. 1854, *C. Belanger 71* (G); St. Pierre, Nov. 1857, *L. Hahn 482* (BM, PI); Martinique, 1868, *T. Husnot 94* (P); Valleé de St. Pièrre, May 1870, *L. Hahn 1057* (K, P); Martinique, 17 Oct. 1919, *A.S. Hitchcock 16454* (US); Tivoli, bords Rivière Matane, 12 Dec. 1943, *H. & M. Stehle 5436* (US); Case Pilote, rivière Case Pilote, 14°38'56,87"N, 61°08'06,19"W, 25 m, 21 Feb. 2017, *C. Delnatte & C. Potiron 3674* (P); Le Vauclin, montagne du Vauclin, Lat. 728313, Long. 1610467, 17 Mar. 2021, *B. Ferlay & G. Viscardi 1172* (P); **Montserrat**. 1879, *P. Duss 769, 770* (NY); Montserrat, 8 Feb. 1907, *J.A. Shafer 701* (NY, US); **St. Lucia**. Shores of Marigot Lagoon, west coast, 21 Mar. 1956, *A.C. Smith 10199* (NY, US); Barre de L'Isle, Castries-Dennery Road, 350-400 m, 14 Apr. 1959, *R.S. Cowan 1572* (NY, US); Mount Durocher 2 miles NW of Patience, 14°N, 61°W, 15 May 1984, *V. Slane 121* (NY); Barre de l'Isle trail to Mt. La Comb, 24 Jan. 1985, *R.A. Howard & al. 19888* (NY, US); **St. Vincent**. St. Patrick Parish, in steep wood of Cacoa, 18 Jan. 1962, *G.R. Cooley 8182* (NY).

(10) *Lasiacis nigra* Davidse, Phytologia 29: 152. 1974. (Fig. 28).

Type: *Costa Rica, Alajuela, 3 km N of Palamares along the Carretera Interamericana, 800 m, edge of coffee plantation, culms 8 m tall, hanging from trees, 22 October 1968, R.W. Pohl & G. Davidse 11272* (holotype: ISC [(photo!) barcode ISC-v-0000548]; isotypes F [(photo!) barcode F0046798F], K! [barcode K000309321], MO! [Acc. No. MO-128800], US! [barcode US00134116]).

(=) *Panicum divaricatum* L. var. *molle* Schlecht. & Cham., Linnaea 6: 33. 1831.

Type: "*Mexico, in sylvis prope Jalapan*, *Deppe & Schiede 892*" (holotype: HAL! [barcode HAL0106583]).

Description

Perennials, caespitose. *Culms* 1-8 m long, erect at the base, arching and clambering into vegetation; *internodes* 0.8-10 mm thick, lignified, glabrous-papillose-puberulent, sometimes papillose-pubescent, hollow; *nodes* glabrous. *Leaf sheaths* pilose or to completely glabrous, margins ciliate with hairs 0.8-3.0 mm long, *auricles* pilose with hairs varying from nearly glabrous to densely pilose; *collars* pilose to glabrous; *ligules* 0.5-2.0 mm long, usually glabrous or occasionally pubescent on the back, apex glabrous to ciliate with hairs 1.5-2.4 mm long; *blades* 5.0-15 cm long, 0.5-2.5 cm wide, linear to lanceolate, usually pilose, puberulent to densely pubescent, often glabrous, base asymmetrical, slightly lobed, clasping the culm, margins scabrid, apex acuminate. *Panicles* 3.0-15 cm long; branches ascending and diverging, up to 9.0-12 cm long, bearing few spikelets; *pedicels* scabrid, spreading at maturity. *Spikelets* (3.5)4.0-5.0(-5.7) mm long, 2.8-4.3 mm wide, obovate, purple when immature; *lower glumes* 1.5-3.0 mm long, 0.4-1.4 mm wide, 5-13-veined; *upper glumes* to 5 mm long, 7-13-veined; *sterile florets* sometimes staminate, *lemmas* 9-12-veined, *paleas* 2/3 to subequal to the length of the fertile floret; *fertile florets* 3.6-5.0(-5.2) mm long, 2.5-3.0 mm wide, brown, *anthers* 2.0-2.8 mm long, whitish, *stigmas* white; *caryopses* 2.5-2.8 mm long, 2.0-2.4 mm wide. *Chromosome number*: $n = 18$ (Davidse 1972, 1974, 1978).

Iconographs

Fig. 106 (Pohl 1980).

Vernacular names

Colombia: "*Guadua silvestre*" *E. Dryander 1895* (US); **Costa Rica**: Cartago, "*caricillo trepador*" *A.*

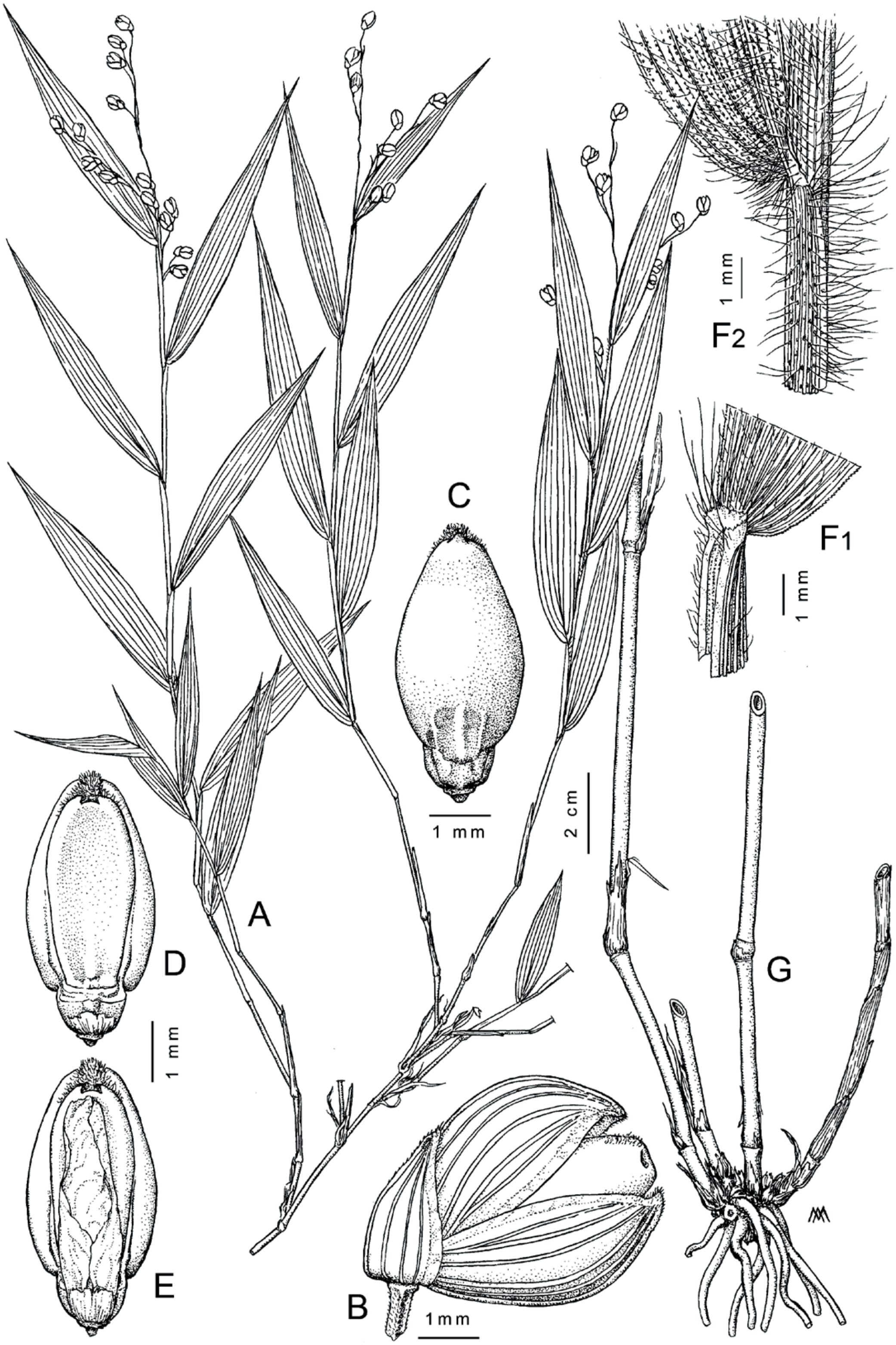

Figure 28. *Lasiacis nigra* Davidse: **A.** Habit. **B**. Spikelet lateral view; **C**. Fertile upper floret dorsal view; **D**. Fertile upper floret ventral view without lower persistent palea; **E**. Fertile upper floret ventral view with lower persistent palea; **F1**. Ligular area pilose [A-F1. from *G.B. Hinton 6722* (K)]; **F2**. Ligular area densely pilose; **G**. Culm at the base with short persistent leaf sheaths [F2-G. from *E.R. Sohns 1198* (K)]. A. *Maury delineavit.*

Tonduz 7234 (G, NY, US); **Ecuador**: Imbabura, "*surillo*" *A. Alvarez & al. 626* (US); **El Salvador**: Chalatenango, "*zacate grande*" *D. Sloot 354* (MO); **Guatemala**: Quezaltenango, "*carrizo*", "*cushcupé*" *P.C. Standley 68268* (US); **Honduras**: "*yakut cincidl*" *Lentz 957* (Lentz 1986); **Mexico**: Colima, "*carrizillo trepador*" *F.J. Santana & al. 5241* (US), "*carricillo*" (Quattrocchi 2006); **Nicaragua**: Managua, "*carricillo*" *A. Garnier 1549* (US).

Distribution

Belize, Bolivia, Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Guyana, Honduras, Mexico, Nicaragua, Panama, Perú, Venezuela. (Fig. 29).

Distribution (bibliographic references)

Davidse (1974, 1978, 1994, 2001, 2004); Steyermark and Huber (1978); Pohl (1980); McVaugh (1983); D'Arcy (1987); Judziewicz (1990); Cialdella and Vega (1996); Serna and López-Ferrari (2000); Zuloaga et al. (2003); Morales (2003); Correa et al. (2004); Bono (1996); Renvoize et al. (2006); Ibáñez et al. (2005); Davidse et al. (2007); Hochke et al. (2008); Sutherland (2008); Bono (2010); Herrera Arrieta et al. (2010) ; Giraldo-Cañas (2011); Dorr (2014); Villavicencio et al. (2014); Villaseñor (2016); Sylvester (2017); Dávila et al. (2018); Sánchez-Ken (2019); Menjivar et al. (2021).

Ecology

Montane and submontane vegetation; common in deciduous shade forest edges, in the underwood, and in pine-oak forests at high elevation (cf. Central America). Elevation between 500 up to 2500 m (Colombia: Antioquia, *R. Callejas P. 11331* (MO); South American collections are often reported in subalpine páramo vegetation in the Andes.

Figure 29. *Lasiacis nigra* Davidse: general geographic distribution.

Phenology

Throughout the year, especially from May through February.

Remarks

Lasiacis nigra, clearly related to *L. maculata* (Davidse 1974, 1978), is more delicate and scandent than *L. maculata*, with a large, open panicle, and long-pedicelled spikelets. Leaves range from nearly glabrous [e.g., see *B. Stergious 19993* (K, US)] to densely pilose [e.g., see *H.E. Stork 2577* (US)]. Davidse (1978) distinguishes a "*small-spikelet form*" from the usual long and open form [e.g., see *G. Davidse 3038* (MO)]. The distribution is more concentrated in Central America and Mexico and spreads in South America to Colombia, Venezuela, Ecuador, Bolivia and Peru, excluding Brazil.

The identification of *Panicum divaricatum* L. var. *molle* Schlecht. & Cham., is confirmed here, a heterotypic synonym of *L. nigra* previously hypothesized by Davidse (1978).

Selected Specimens

BELIZE. **Cayo**. Comune Ridge, Jun.-Aug. 1936, *C.L. Lundell 6434* (C, NY, US); Cayo, Maya Mountains, Smokey Branch, 850 m, 16°33'N, 89°02'W, 18 Mar. 1994, *A. Monro & T. Helgason 409* (BM, MO); March/4 way up Ceibo Chico track, 670 m, 16°32'N, 89°05'W, 1 Mar. 2000, *M. Short & al. 222* (BM, MO); Maya Mountain divide in the vicinity of Doyle's Delight, the highest point in the Country, along North Ridge Trail, 1000-1100 m, 16°29'N, 89°02'W, 22 Aug. 2007, *B.K. Holst & C. Young 9002* (MO); **Toledo**. Union Camp, 12 May 1979, *C. Whitefoord 1676* (BM); Little Quarz Ridge, 5.5 km E of Union Camp, 980-1035 m, 16°24'02"N, 89°06'40"W, 21 Feb. 1997, *T. Hawkins 1531A* (MO).

BOLIVIA. **Cochabamba**. Chapare, 29 Jan. 1929, *J. Steinbach 8976* (G); **Chuquisaca**. Sud Cinti, Cañon Chapirenda, ca. 5 km al NW de la Comunidad de Las Abras, Camino a Candado Grande, 1372 m, 21°04'24"S, 64°15'35"W, 26 Jan. 2006, *R. Lozano & J. Peñaranda 1922* (MO); **Cundinamarca**. Caqueza, Bogotà, s.d., *Karsten s.n.* (W); **Santa Cruz**. Florida, 10 km E of Samaipata, 23 Mar. 1981, *S.A. Renvoize & T.A. Cope 4045* (US).

COLOMBIA. **Antioquia**. Quebrada de Musingita, W of Frontino, 1580 m, 27 Mar. 1944, *E.L. Core 477* (US); Cerca al camino viejo a Ríonegro, 7 km E of Medellín, 2100 m, 13 Feb 1949, *A. Molina & F.A. Barkley 76* (BM); Jardín, Vereda Las Manguitas, 1500 m, 19 Sep. 1986, *R.W. Pohl & J. Betancur 15567* (MA, MO, US); Sonson, km 18 of road Sonson-La Union, 2170 m, 05°49'N, 75°17'W, 8 Mar. 1987, *J.L. Zarucchi & N. Bedoya 4594* (MO); Medellín, Via Santa Melena, 75°20'W, 6°10'N, 26 Mar. 1987, *R. Callejas & O. Escobar 3311* (NY); Salgar, km 13.5 between Salgar-El Douro (Chocò), 05°59'N, 76°06'W, 30 Apr. 1987, *J.L. Zarucchi & al. 6068* (NY); Andes, 6 km de Andes hacia Vereda Momblan, 1480 m, 23 Aug. 1988, *R. Fonnegra & al. 2400* (MO); 8-15 km de Amalfi a Rumazon, sitio "Salazar" y "La Playa", Cordillera Central, 1550 m, 06°56'N, 75°04'W, 28 Sep. 1988, *J. Betancur & al. 767* (MO); Urrao, Corregimiento Santa Isabel, via a la Finca La Palma, 15 km E de Urrao en la Troncal a Medéllin, 2020 m, 6°10'N, 76°15'W, 10 Apr. 1989, *R. Callejas & al. 7913* (MO, NY); Medellin, 8-12 km SE de Medellin en la via a la Ceja, alrededores del alto de la Pova, cuenca de quebrada "La Poblada", 2350-2500 m, 06°13'N, 75°35'W, 13 Nov. 1994, *R. Callejas P. 11331* (MO); Betania, Farallones del Citará, paraje Las Canos, 1730 m, 5°44'N, 76°00'W, 12 Nov. 1997, *R. Fonnegra & al. 6603* (US); **Caldas**. Salento, 1600-1900 m, 25-31 Jul. 1922, *E.P. Killip & T.E. Hazen 8770* (NY, US); **Cauca**. Hills of Miraflores above Palmira, Cordillera Central, 1200-1600 m, Jan. 1906, *H. Pittier 886* (US); Río Sucio, Cauca Valley, 1500-1600 m, 27 Jun. 1922, *F.W. Pennell & E.P. Killip 7223* (NY), *7227* (US); El Tambo, 1700 m, 25 Jul. 1934, *K. von Sneidern 164* (US); **Chocó**. Carretera Ansernuevo-San José del Palmar, límite con el Valle del Cauca, Alto del Galapago, 28 Aug. 1976, *E. Forero & R. Jaramillo 2231* (MO, NY); **Cundinamarca**. Salto de Tequendama, dense forest of La Hondonada, 2250-2300 m, 2 Oct. 1938, *J. Cuatrecasas 221* (US); 1 km S of Pandi, 12 Feb. 1983, *J.R. Wood 4110* (K); Buenavista, NW of San Cajetano, 22 May 1983, *J.R. Wood 3756* (K); By the Camino Road from Soacha to Santandeocito, 19 May 1985, *J.R. Wood 4392* (K, US); **El Valle**. Dagua, 11 May 1922, *E.P. Killip 5444* (NY, US); Pavas, 1700-2100 m, 24-29 Sep. 1922, *E.P. Killip 11649* (US); La Cumbre, 7-10 May 1922, *F.W. Pennell 5025* (NY, US); Las Nieves, Cordillera Occidental, May 1937, *E. Dryander 1895* (US); Cordillera Occidental, Hoya del Río Digua, pietra de Moler, 900-1180 m, 19-28 Aug. 1943, *J. Cuatrecasas 14980* (US); El Valle, 8 Dec. 1943, *J. Cuatrecasas 15358* (BM, US); El Valle, Cordillera Occidental, monte La Guarida, filo de la cordillera sobre La Carboneria (entre Las Brisas y Alban), 1950-2000 m, 16 Oct. 1946, *J. Cuatrecasas 22174* (US); Valle del Cauca, Sevila, Cordillera Central, Las Brisas, 2000 m, 10 Apr. 1979, *J. Cuatrecasas 28941* (US); Bosque de Neblina, Finca Torremolinos, km 22 carretera entre Cali y Buenaventura, 13 Oct. 1982, *L. de Escobar & al. 2690* (MO, NY); Ansermanuevo-San José del Palmar, 30-37 km W of Ansermanuevo, 1850-1875 m, 40°40'N, 76°25'W, 13 May 1984, *J.L. Luteyn & al. 10396* (MO, NY); Restrepo, Vereda de Roman, cerca de Río Grande, por la carretera entre Pavas y Restrepo, en predios de la Familia Reyna, 22 May 1988, *J.E. Ramos & al. 984* (MO); La Elvira, Finca Zingara, 1600-1700 m, 3°28'N, 76°37'W, 25 km W of Cali, 20 Apr. 1989, *J.L. Luteyn & al. 12548* (K, MO, NY, US); N of Calima, 1700 m, 6 Sep. 1992, *S.A. Renvoize 5370* (K, US); **Huila**. Cordillera Oriental, E of Neiva, 1300-1800 m, 1-8 Aug 1917, *H.H. Rusby & F.W. Pennell 861* (MO), *963* (NY, US); Quebrada Ariari above Galilea, 23 km ENE of Colombia, 2000 m, 3°28'N, 74°38'W, 28 Dec. 1942, *F.R. Fosberg 19635* (US); **Magdalena**. Santa Marta, 1898-1901, *H.H. Smith 2144* (MO, US); Sierra de Perijá, E of Manaure, Hoya del Río Manaure, San Antonio, 1700 m, 14 Nov. 1959, *J. Cuatrecasas & R. Romero Castaneda 25306* (US); Magdalena, Sierra Nevada de Santa Marta, along edge of Quebrada Indiana, 10°59'N, 73°58'W, 27 Aug. 1972, *J.H. Kirkbride 1931* (NY); Magdalena, Sierra Nevada de Santa Marta, at the edge of forest between Quebrada Rotella and finca Los Arroyitos, 1650-1700 m, 10°56'N, 73°58'W, 27 Sep. 1972, *J.H. Kirkbride 2223* (MO, US); **Nariño**. Pasto, 2600 m, 30 Apr. 1939, *A.H.G. Alston 8292* (US); Buesaco, on Río Pajajoy, 22 km NE of Pasto, 2400 m, 1°22'N, 77°10'W, 24 Apr. 1943, *F.R. Fosberg 20532* (US); Alrededores de Samaniego, 10 Jan. 1952, *A. Fernández & L.E. Mora 1188* (NY); Entre Cartago y la Union, 1750 m, 27 Oct. 1962, *L.E. Mora 2407* (US); Reserva La Planada, quebradas El Mar-La Calladita, 1500-1800 m, 01°10'N, 77°58'W, 30 Apr. 1988, *O. de Benavides 9707* (MO); Ricaurte, vicinity of Ricaurte, along Río Imbì, 1150 m, 01°08'N, 77°56'W, 16 Mar. 1990, *T.B. Croat 71510* (MO); **Risaralda**. Pereira, Hacienda Los Cristales, lomas en orilla derecha de Río Cauca, 1200 m, 04°53'N, 75°50'W, 1 Jan. 1995, *P. Silverstone-Sopkin & N. Paz*

7266 (MO); **Santander**. Vicinity of California, 2000 m, 11-27 Jan. 1927, *E.P. Killip & A.C. Smith 17013* (NY, US); **Tolima**. Libano, 1300-1500 m, 26-29 Dec. 1917, *F.W. Pennell 3415* (K, MO, NY, US); Tolima, Km 23 de la via Venadillo-Sta. Isabel, costado oriental de la Cordillera Central, 1710 m, 4°43'N, 75°5'W, 27 Jan. 1987, *X. Londoño & I.D. Quintero 56* (MO, US), *57* (MO).

COSTA RICA. **Alajuela**. Vicinity of Fraijanes, 12-13 Feb. 1926, *P.C. Standley & R. Torres 47507* (US); Vicinity of San Ramon, La Palms de San Ramon, 12 Jul. 1926, *A.M. Brenes 5191* (NY, US); Santa Clara Hills, 16 Jun. 1928, *H.E. Stork 2577* (US); Vicinity of San Ramon, Calera de San Ramon, 21 Jan. 1935, *A.M. Brenes 20314* (NY); Vara Blanca de Sarapiqui, north slope of Central Cordillera, Jul.-Sep. 1937, *A.F. Skutch 3148* (K, NY, US); San Luis de Zarcero, 11 Aug. 1938, *A. Smith 41015* (MO, NY); 6.5 km W of Varablanca, 1950 m, 10 Aug. 1966, *R.W. Pohl & C. Calderón 10280* (USJ); Cordillera Central, Volcán Potás, 10 km above Vara Blanca by road, 29 Sep. 1968, *R.W. Pohl & G. Davidse 11174* (K, US); 11 km S of Ciudad Quesada along Highway, 15 Oct. 1968, *R.W. Pohl & G. Davidse 11250* (K, US); 10 km N of San Ramón along Interamericana Highway, 22 Oct. 1968, *R.W. Pohl & G. Davidse 11275* (K, US), **n = 18!** (Davidse 1978); La Palma de San Ramón, 31 Oct. 1968, *R.W. Pohl & G. Davidse 11371* (K, US); San José, 2 km SE of Barbacoas, 7 Nov. 1968, *R.W. Pohl & G. Davidse 11403* (K, US); Along road from San Ramón northward through Balsa, ca. 5.7 km N of bridge over Quebrada Volio, SW of road, ca. 10°08'N, 84°29'W, 10 Sep. 1979, *W.D. Stevens 14103* (K, MO, NY); Monteverde Reserve, Atlantic slope, Río Peñas Blancas valley, 20 Oct. 1984, *W.A. Haber 718* (MO, NY); Reserva Biológica Monteverde, 1000 m, 10°18'58"N, 84°42'42"W, 25 Sep. 1990, *N. Obando 136* (USJ); **Cartago**. Cartago, Nov. 1887, *J.J. Cooper 98* (G); Cartago, Dec. 1896, *A. Tonduz 7234* (G, NY, US); Vicinity of Santiago, 20 Apr. 1906, *W.R. Maxon 128* (NY); Vicinity of Cartago, Feb. 1924, *P.C. Standley 33365* (NY, US); La Estrella, 26-27 Mar. 1924, *P.C. Standley 39215* (US); Along the Río Reventado, 26 Feb. 1926, *P.C. Standley & J. Valerio 49448* (US); Cordillera de Talamanca, S of Moravia de Chirripó, 9 Aug. 1968, *R.W. Pohl & G. Davidse 10870* (K, US), **n = 18!** (Davidse 1978); 12 km NE of Pacayas along Highway 230, 10 Aug. 1968, *R.W. Pohl & G. Davidse 10889* (F, K, US); Cordillera de Talamanca, 25 km SW of Tejar along the Carretera Interamericana, 24 Sep. 1968, *R.W. Pohl & G. Davidse 11134* (K, US), **n = 18!** (Davidse 1978); Canyon of the Río Grande de Orosí, 9 mi. S of Purasil, 3 Oct. 1968, *R.W. Pohl & G. Davidse 11198* (K, US); 3 km W of Grano de Oro, E of the Río Pacare, 21 Nov. 1968, *R.W. Pohl & G. Davidse 11477* (K, US); Edge of Río Naranjo, 3 km E of Cachì, 11 Jun. 1969, *R.W. Lent 1736* (NY); 3 km up montain from Tejar, 10 Aug. 1972, *J. & C. Taylor 11866* (MO, NY, US); Hacienda Linda Vista, just S of Dulce Nombre de Culmi, SE of Cartago, 22 Nov. 1983, *E. Judziewicz 4377* (MO); Hills at N side of Río Navarro between Río Sombrero and Quebrada Solon, W of El Muñeco, 1260-1600 m, 9°55'N, 83°48'W, 15 Nov. 1987, *M. Grayum 8450* (MO); **Guanacaste**. Parque Nacional Rincon de la Vieja, the SE slopes of Volcán Santa Maria, above Estación Hacienda Santa Maria, 900-1200 m, 10°47'N, 85°18'W, 27-28 Jan. 1983, *G. Davidse & al. 23370* (MO); Cebadilla, Abangares, 1400 m, 21 Jul. 1985, *W.A. Haber & E. Bello C. 2266* (MO); Canton de Liberia, P.N. Rincon de la Vieja, Cordillera de Guanacaste, Sector Santa Maria, sendero La Plantacion, cabeceras Quebrada Zopilote, 950-1100 m, 10°46'50"N, 85°17'55"W, 14 Aug. 1996, *J. Morales 5654* (MO); Canton de Liberia, P.N. Guanacaste, cuenca del tempisque, 5 km antes de Cacao, a orilla de calle, 1100 m, 10°55'45"N, 85°29'05"W, 16 Jan. 1998, *A. Soto 112* (MO); **Heredia**. Cliffs above road to Puente Mulas, S of San Antonio, 27 Oct. 1968, *R.W. Pohl & G. Davidse 11351* (K, US); San José de la Montaña, Finca frente a la Lorena, 26 Nov. 1972, *M. Montiel 048156, 048157, 048158* (USJ); Santo Domingo, Cuenca del Tarcoles, Finca por el Río Tures, ca. 1 km linea recta al SE de San Francisco de San Isidro de Heredia, 1250 m, 9°59'53"N, 84°04'03"W, 19 Dec. 2004, *B. Hammel 23541* (MO); **Limón**. 19 miles by road below Turrial on road to Siquirres, 16 Aug. 1966, *R.W. Pohl 10310* (NY); Limón Z.P. Río Banano, cerca 11 km SW del pueblo de Aguas Zarcas, 9°49'35"N, 83°10'02"W, 1200-1300 m, 25 Oct. 2002, *D. Solano 4709* (PMA); Limón, Limon Z.P. Río Banano, Cuenca del Banano, 9°48'56"N, 83°09'35"W, 1200 m, 26 Oct. 2007, *A.K. Monro 5827* (PMA); **Puntarenas**. Peninsula Osa ad Golfo Dulce, circa Puerto Jimenez, versus Sto. Domingo, 10 Apr. 1930, *O. Porsch 180* (G, W); Cañas Gordas, 27 Sep. 1968, *R.W. Pohl & G. Davidse 11166* (K, US); Primary forest above coffee fincas along Río Coto Brus, near Coton, 23 km N of La Union (on Panamá border), 9 Aug. 1974, *T.B. Croat 26615* (MO); Monteverde, 20 Jun. 1976, *R.W. Pohl & R. Pinette 13250* (K, MO, NY); Isla Violín, Sierpe, 10 May 1977, *J. Gomez Laurito 2655* (USJ); Monteverde village, 25 Aug. 1981, *D.N. Hepper 13* (BM); Monteverde Village, Aug. 1981, *D.N. Hepper 54* (BM); Forest along trail between Las Alturas and Cotonsito, 1400 m, 08°56'30"N, 82°48'W, 31 Aug.-1 Sep. 1983, *G. Davidse 24655* (K, MO); Foothills of the Cordillera de Talamanca, lower montane forest in the area of Sitio Coton (Cotonsito), along the road to Sitio Coto Brus, 8°57'N, 82°46'W, 3-4 Sep. 1983, *G. Davidse 24620* (PMA, US); Monteverde, Cloud Forest Reserve, Cordillera de Tilaran, 1500-1620 m, 13 Jul. 1984, *W.Z. Pounds 270* (MO); Canton de Coto Brus, Z.P. Las tablas, Cordillera de Talamanca, Quebrada Pizote, Finca Cafrosa, San Vito, 1200 m, 08°54'40"N, 82°47'10"W, 22 Sep. 1990, *M. Ramírez 105* (MO); Coto Brus, Las Crucis Biological Station, San Vito, margins of trail to Río Jaba, 1275 m, 8°47'08"N, 82°57'27"W, 26 Jun. 1994, *W.J. Kress & C.M. Christy 94-3973* (US, USJ); Cantón de Buenos Aires, cuenca Térraba-Sierpe, 1766 m, 9°02'21"N, 83°00'35"W, 1 Jun. 1996, *J. Quesada 1646* (K, MO, NY); Canton de Coto Brus., Z.P. Las Tablas, cuenca Terraba-Sierpe, camino a Cotoncito, 1520 m, 8°56'25"N, 82°47'37"W, 15 Dec. 1997, *B. Gamboa R. 2064* (MO); Coto Brus. Z.P. Las Tablas, Cuenca Térraba-Sierpe, 26 Jul. 2000, *V. Ramírez 2231* (G); Estacón Biológica de la Reserva dé Monteverde, 1500 m, 23 Apr. 2001, *W.A. Haber 4/2001* (USJ); Buenos Aires, Parque nacional de La Amistad Cuenca Térraba-Sierpe, 9°07'07"N, 83°05'07"W, 1600-1700 m, 24 Feb. 2008, *A. Rodriguez 11956* (MO, PMA); **San José**. Uruca près San José, 26 Nov. 1892, *A. Tonduz 7207* (NY, P, US); Vicinity of La Palma, on the road to La Hondura, 17-18 Jul. 1923, *W.R. Maxon & A.D. Harvey 7998* (NY, US); Río Tirribi, 11 Feb. 1924, *A. Alfaro 33989* (US); Between San Pedro Montes de Oca and Curridabat, 5 Dec. 1925, *P.C. Standley 41296* (US); San José, vicinity of Santa Maria de Dota, 14-26 Dec. 1925, *P.C. Standley 41665* (US); Vicinity of Santa Maria de Dota, 26 Dec. 1925–3 Jan. 1926, *P.C. Standley & J. Valerio 43476* (US); San José, finca "Los Helechales", between Buenos Aires and Cerro Pittier, 1700 m, San José, minor road 4 mi SW of División, 1775 m, 13 Feb. 1966, *W.H. Hatheway 1689* (US); 16 Jul. 1966, *R.W. Pohl & C. Calderón 10070* (MO, USJ); San José, road between Aserrí and Tarbaca, 1675 m, 22 Aug. 1966, *R.W. Pohl & C. Calderón 10388* (USJ); San José, 7 km S of Aserrí, 6 Sep. 1968, *R.W. Pohl & G. Davidse 11041* (K, US); 2 km NNE of San Gabriel, 6 Sep. 1968, *R.W. Pohl & G. Davidse 11050* (US), *11051*, (K, US), **n = 18!** (Davidse 1978); Río La Hondura below La Hondura, 4 Oct. 1968, *R.W. Pohl & G. Davidse 11214* (K, US); Near Terbaca at 1750 m, 30 Aug. 1971, *W.C. Burger & M. Burger 8402* (PMA); Forest on Cerro Pico Branco, 9°52'N, 84°08'W, 4 km S of Escazú, 2000 m, 12 Dec. 1976, *R.W. Lent 3981* (PMA); Between Bajo La Hondura and Alto La Palma, 10°2'N, 83°59'W, 1400-1500 m, 17 Jul. 1983, *K. Barringer & al. 3924* (PMA); Cerros de Escazú, El Mesón, 1550 m, 9°52'15"N, 84°05'50"W, 11 Sep. 1993, *J.F. Morales 1673* (BM, MO); Dota, Santa Maria, 22 Oct. 1998, *A. Estrada 1843* (K); Canton de Terrazu, cuenca del naranjo y Paquita, La Virgen, cabeceras Río Palo Seco, sector SW, 1100 m, 9°36'00"N, 84°08'25"W, 28 Apr. 1999, *J. Morales 7065* (MO); Acosta, Sabanillas, 3 Oct. 2001, *R. Chacón 146* (K); Turrubares, San Juan De Mata, 9°45'14"N, 84°35'35"W, 27 Nov. 2001, *R. Chacón 213* (K, MO); **Turrialba**. Torre Alta, Fila Cruces, road to Paraguas, Finca Gamboa, 1450 m, 5 Mar. 2001, *F. Werner 188* (USJ).

ECUADOR. **Azuay**. Steep forested slopes bordering Río Norcay between Río Gamolotal and Río Norcay, 1095-1370 m, 7 Jun. 1943, *J.A. Steyermark 52868* (US); **Carchi**. Cerro Golondrinas, Upper Río Pablo drainage, along crest of ridge to N of river, very wet, primary cloud forest, 1740-1780 m, 00°53'N, 78°10'W, 24 Apr.-2 May 1993, *B. Boyle & L. Dalmau 1798* (MO); **Chimborazo**. Huigra, 1300 m, 20 Jul. 1923, *A.S. Hitchcock 20754* (NY, US); **Cotopaxi**. 3 km E of El Palmar on road Quevedo-Latacunga, 800 m, 5 Apr. 1980, *C.H. Dodson & A. Gentry 10230* (MO); Tenefuerste, Río Pilalo, km 52-53, Quevado, Latacunga, 750-1300 m, 7 Feb. 1982, *C.H. Dodson & A.H. Gentry 12245* (MO, US); **Esmeraldas**. Quininde, Bilsa Biological Station, Montañas de Mache, 20 km NW of Quinindé and 3 km W of Santa Isabela, 600 m, 00°22'N, 79°45'W, 14 Sep. 1994, *J.R. Abbott 15140* (MO); Along road from Lita to San Lorenzo, vicinity of Alto Tambo, 841 m, 00°33'53"N, 78°32'36"W, 21 Feb. 2005, *T.B. Croat 95117* (MO); **Imbabura**. Between Otavalo-Selva Alegre, 78°34'W, 00°15'N, 13 Mar. 1988, *S. Lægaard & S.A. Renvoize 70821* (K); Along road Otavalo-Apuela, 3 Jul. 1991, *H. van der Werff & al. 12172* (MO, US); Cotacachi, La Florida, 1900-2500 m, 00°23'S 78°28'W, 28 Aug. 1992, *A. Alvarez & al. 626* (US); Cotacachi, Parroquia Garcia Moreno, Reserva Biologica Los Cedros, 1690 m, 00°17'28"N, 78°47'13"W, 28 Oct. 2005, *H. Vargas & al. 6355* (MO); **Loja**. Santiago Zamora, Canillones, Río San Francisco, 1700-1750 m, 3°56'S, 78°57'W, 20 Feb. 1945, *F.R. Fosberg 23149* (US); Cerro Campana, 7 km from Vilcabamba, on road to Yangana, ca. 1900 m, 04°17'S, 79°16'W, 17 Jun. 1979, *B. Løjtnant & al. 14986* (MO); Km 30 Malacatos-El Tambo-Catamayo, 4 Apr. 1998, *S. Lægaard 18630* (K); Near Sozoranga, 30 Nov. 1999, *S. Lægaard & al. 20856* (K); Vicinity of Mercadillo, at El Retiro, 1500-1700 m, 79°59'W, 04°00'S, 13 Aug. 2000, *J.E. Madsen & al. 7085* (MO, NY); **Los Ríos**. 9 km E of Patricia Pilar, 58 km ENE of Quevedo, on Pan-American Highway to Santo Domingo de Los Colorados, 00°36'S, 79°18'W, 1 Jul. 1977, *H.H. Iltis & M.G. Iltis 86* (MO); **Napo**. Carretera Hollin-Loreto-Coca, 700-750 m, 00°40'S, 77°30'W, 8 Dec. 1987, *V. Zak & J. Jaramillo 3124* (C, K, MO, NY, US, W); Napo, Archidona Canton, Parque Nacional Sumaco y Comunidad de Pacto Sumaco, 1550-1700 m, 00°38'56"S, 77°35'49"W, 26 Apr. 1997, *A. Alvarez & al. 2019* (MO); Along road from Baeza to El Chaco, vicinity of Río Sardinas Grande, along Río Quijos, disturbed area, 6 km NNE of San Francisco Borja, 1767 m, 00°22'32"S, 077°49'01"W, 17 Apr. 2003, *T.B. Croat 87675* (MO, US); **Oro**. Between La Chorita and Portobelo (Gold Mine near Zaruma), 1000-2000 m, 28 Aug. 1923, *A.S. Hitchcock 21184* (US); **Pastaza**. Between Puyo and Canelos, 325-375 m, 1-3 Feb. 1935, *Y. Mexia 6850* (US); Vicinity of Puyo, 750-1000 m, Aug. 1939, *A.F. Skutch 4397* (K, MO, NY, US); 20 km S of Puyo on road to Macas, across from entrance to Colonia Ventana, ca. 1050 m, 01°34'S, 77°54'W, 8 Apr. 1989, *W.W. Thomas & M. Rios 6682* (MO); Towards Arajuno, 19 Sep. 1998, *S. Lægaard & I. Grignon 19171* (K); **Pichincha**. Chiriboga on road from Quito to Santo Domingo de los Colorados, 1800 m, 11 Nov. 1939, *E. Asplund 8669* (G, K, NY, UPS, US); Pichincha, Nanegalito al NO de Tandayapa, 1300 m, 15 Jul. 1950, *M. Acosta Solís 17148* (US); Road Nono-Pacto-Río Yacuambi, 5-10 km above Nanegalito, 21 Jul. 1980, *L. Holm-Nielsen & al. 24430* (K); Km 15 on road Alluriquin-Chiriboga-Quito, 1350 m, 78°51'W, 00°17'S, 20 Oct. 1985, *S. Lægaard 55479* (BM, C, G, K, MA, MO, NY, P, UPS, US, W); Carretera Quito-Aloag-Santo Domingo de los Colorados, 1400-2000 m, 00°21'30"S, 78°51'15"W, 7 Jun. 1986, *V. Zak 1037* (K, MO, NY, US); Reserva Floristica-Ecologica "Río Guajalito", km 59 de la carretera Antigua Quito-Sto. Domingo de los Colorados, 1800-2200 m, 78°48'W, 00°13'53"S, 22 Sep. 1986, *V. Zak 1272* (G, MO, US); Carretera Antigua Quito-Santo Domingo, 1800-2200 m, 00°13'S, 78°48'W, 10 Oct. 1988, *V. Zak & J. Jaramillo 3858* (BM, MO, NY); 13 km E of Alluriquin, 32 km E of Santo Domingo), on new road to Quito, 980 m, 5 Jun. 1990, *P.M. Peterson & E.J. Judziewicz 9533* (MO); Canton Quito, Parroquia Nanegal, Reserva Maquipucuna, 00°08'N, 78°38'W, 7 Jan. 1995, *G.L. Webster 31039* (MO, NY); Along road from Tandayapa to Nono, 1681 m, 00°00'18"N, 78°40'24"W, 13 Feb. 2005, *T.B. Croat 94556* (MO, US); **Tungurahua**. Valley of Pastaza River, between Banhos and Cashurco, 8 hours E of Banhos, 1300-1800 m, 25 Sep. 1923, *A.S. Hitchcock 21856* (US); Road Baños-Puyo, 22 km from tunnel at Agoyan 1370 m, 0124'S, 7813'W, 1 Dec. 1984, *S. Lægaard 53395* (MO); **Zamora-Chinchipe**. E of Los Encuentros along the road to Jardin del Condor, 17 Jun. 1998, *S. Lægaard & al. 18919* (K); Zamora-Chinchipe, along road from Zamora to Bombuscaro, 2 Sep. 1998, *S. Lægaard 19099* (K); Zamora-Chunchipe, along road from Namirez to Nambija, 3 km above San Carlos, 762 m, 03°46'44"S, 78°38'30"W, 28 May 2003, *T.B. Croat & M. Menke 89584* (MO).

EL SALVADOR. **Ahuachapán**. San Fco. Menendez, Hacienda San Benito, Cerro Davila, cafetal de Rafaela Davila, 13°49'N, 89°56'W, 15 Nov. 1991, *E. Sandoval 13* (MO); El Impossible Reserva, Campana, 1400 m, 13°51'N, 89°54'W, 24 Jun. 1998, *A. Monro & al. 1987* (BM, MO); **Chalatenango**. La Palma area, Caballero, 900-1500 m, 14°18'N, 89°08'W, 9 Nov. 2001, *D. Sloot 354* (MO); **La Libertad.** Volcano of San Salvador, 20-26 Nov. 1911, *A.S. Hitchcock 8925* (US), *8951* (K, NY, US), *8952* (NY, US), *8962* (US); Santa Tecla, slopes of Volcán San Salvador, 15 Jan. 1949, *L.O. Williams & A. Molina 15100* (US); Volcán de San Salvador, ca. 1 km S of El Boquerón crater, 6 Jun. 1970, *G. Davidse & R.W. Pohl 2025* (K, L, MO, NY, US), **n = 18!** (Davidse 1978); Volcán de San Salvador, 24 Jun. 1978, *R.W. Pohl & M. Gabel 13661* (K, MO); Carretera a Comasagua, 10 Jan. 1996, *E.A. Montalvo 6410* (K); La Libertad, Teotepeque, 4 May 1996, *J. González 334* (K); San Salvador, Volcán San Salvador, El Boquerón, 4 Feb. 1998, *A. Monro & al. 2194* (BM); El Boquerón, Parque Nacional El Boquerón, falda volcàn de San Salvador, 25 Oct. 2015, *J. Menjívar & R.M. Baldini 3403* (FT, LAGU, MHES); **Morazán**. Summit of second peak from eastern end, Montes de Cacaguatique, 2 Jan. 1942, *J.M. Tucker 693* (G, NY, US); NE of finca of General J.T. Calderón, Montes de Cacaguatique, 6 Jan. 1942, *J.M. Tucker 733* (K, US); **Santa Ana**. E side of lago de Coatepeque, 900 m, 8 Jun. 1970, *G. Davidse & R.W. Pohl 2035* (MO); Along dirt road between Metapán and Cerro Monte Cristo, 7 miles NE of Metapán between Administrative Office and Los Planes, 1200 m, 30 Jul. 1977, *T.B. Croat 42290* (MO); Cerro Verde, 17 Jun. 1978, *R.W. Pohl & M. Gabel 13594* (K, L, MO, NY); Cerro Verde National Park, 2300 m, 13°29'N, 88°32'W, 23 Jan. 1998, *K. Sidwell & al. 407* (BM, MO); Parque Nacional Los Volcanes, Los Andes, sector Santa Elena, 1810 m, 13°51'N, 89°37'W, 18 Jul. 2006, *D. Rodriguez 272* (MO); Parque Nacional Montecristo, El Murón, Cárcava No. 1, 14°23'36"N, 89°22'43"W, 1697 m, 10 Feb. 2016, *J. Menjívar & R.M. Baldini* **3517** (FT, LAGU, MHES); **San Miguel**. Volcán San Miguel, finca Mascota, 13°26'48"N, 88°15'92"W, 5 Feb. 1999, *K. Sidwell & al. 887* (BM, MO); **San Vicente.** Volcán de San Vicente, 7-8 Mar. 1922, *P.C. Standley 21508* (US); **Sonsonate**. Sierra Apaneca, cut over forest Cerro El Pilón, 23 Feb. 1968, *A. Molina & E.A. Montalvo 21605* (NY).

GUATEMALA. **Alta Verapaz**. Coban, 14 Feb. 1941, *F.W. Hunnewell 17091* (NY); 5 km NW de Cobán, 10 May 1963, *A. Molina & A.R. Molina 11987* (US); 10 km S of Coban, 9 Mar. 1970, *W.E. Harmon & J.D. Dwyer 4278* (MO); **Baja Verapaz**. Union Barrios, 10 Aug. 1975, *C.L. Lundell & E. Contreras 19598* (MO, NY); **Chimaltenango**. Along road from Chimaltenango San Martin Jilotepeque, 25 Nov. 1938, *P.C. Standley 57903* (NY); **Chiquimula**. Transecto La Hondonada, 300-400 m, 14°51'03"N, 89°31'08"W, 22 Sep. 2003, *M. Véliz 14498* (MO); **El Progreso**. Hills around Barranquillo, 650 m, 17 May 1942, *J.A. Steyermark 46406* (US); **Guatemala**. Guatemala City, 2 Feb. 1905, *W.A. Kellerman 4735* (US); Guatemala City, 1-3 Dec. 1911, *A.S. Hitchcock 9057* (US); 10 km S of San Raimundo, 18 Jan. 1939, *P.C. Standley 62918* (US); Along River Villalobos, 12-23 Jan. 1966, *A. Molina & al. 16067* (NY, W); Aldea Lo de Coy, km 21 on Highway between San Lucas and Guatemala City, 14 Nov. 1967, *A. Molina 21108* (NY); Panajachel to Monte Mercedes trail, 9 Aug. 1979, *J.D. Boecke & S. Utzschneider 2862* (K, MO, NY); **Huehuetenango**. Along road 13 km W of Huehuetenango, near Puente de Xinaxó, 30 Dec. 1940, *P.C. Standley 81531* (K); Near crossing of Rio San Juan Ixtán, E of San Rafael Pétzal, 1730 m, 9 Jan. 1941, *P.C. Standley 82866* (US); Cerro Huitz, between Mimanhuitz and Yulhuitz, Sierra de los Cuchumatanes, 1500-200 m, 14 Jul. 1942, *J.A. Steyermark 48627* (US); 10-20 km W of Huehuetenango, 3 Dec. 1963, *L.O. Williams & al. 22295* (G, US); Near El Reposo, about 8 km from Mexican frontier, 900-1000 m, 14-18 Dec. 1972, *L.O. Williams & al. 41246* (MO); Benedicion de Dios, Aldea, Montaña Virgen, remanente de Bosque en la Montaña Virgen, 1560 m, 16°01'18"N, 91°32'22"W, 12 Dec. 2006, *M. Garcia 2401* (MO); Nebton, Aldea La Trinidad, roadside through moist forest along the road to Nuevo San José Frontera along crossing of Arroyo Salchila Creek, 1500 m, 15°59'N, 91°34'W, 6 Mar. 2009, *J.M. Maarten & al. 5568* (MO); Puente Selegua II. Cerca Del Camino, Paredones de Piedras, Santa Ana Huista, Huehuetenango, 1500 m, 15°27'41"N, 91°46'31"W, 7 Dec. 2006, *A. Soto 1463* (MO); **Izabal**. Livingston, Rio Dulce, Mar. 1889, *J. Donnell Smith 1852* (US); Los Amates, 29 May 1919, *S.F. Blake 7721* (US); Montañas del Mico, 11 km W of Santo Tomás de Castilla, 8 Sep. 1988, *W.D. Stevens & al. 25492* (BM, MO); W of Santo Tomas de castilla, near Guatel antennas on one of the summits of Cerro San Gil, humid evergreen forest on slopes, 800-900 m, 15°40'N, 88°41'W, 21 Sep. 1997, *M. Nee & al. 47330* (MO); **Quezaltenango**. Volcán Zunil, 5700 ft, 8 Aug. 1938, *A.F. Skutch 986* (US); Finca Pireneos, below Santa María de Jesús, 1350-1380 m, 11 Mar. 1939, *P.C. Standley* 68268 (US); Along old road between Finca Pirineos and Patzulín, 9 Feb. 1941, *P.C. Standley 87067* (K) *86807* (NY); Between Colomba and Las Mercedes, 600-900 m, 20 Feb. 1941, *P.C. Standley 87968* (US); Mountains above Río Samalá, Sierra Madre Mts., 2 km W of Zunil, 14 Dec. 1962, *L.O. Williams & al. 23032* (G, NY, US, W), *22982* (G); San José Buena Vista, Costa Cuca, 900 m, 26 Jan. 1980, *L. Rodriguez 1777* (P); Along Highway Cito N of junction with CA2, toward Quezaltenango, in watershed reserve INDE "Santa Maria", km 199, loose gray soil, steep slopes W of Highway, 14°45'N, 91°32'W, 22 Jan. 1987, *T.B. Croat & D.P. Hannon 63424* (MO); **Quiché**. By Río Cataratas, 3 km N of Nebaj, 26 Dec. 1978, *M.J. Metzler 37* (MO); Chel, Camino a Amacchel, Bosque, ChaJul., Quiché, 1553 m, 15°41'16"N, 90°59'34"W, 26 Jul. 2006, *M. Garcia 1818* (MO); **Sacatepéquez**. Above Pastores, 23 Dec. 1938, *P.C. Standley 60762* (K); Sacatepéquez, barranco above Dueñas, 1590-1800 m, 21 Jan. 1939, *P.C. Standley 63194* (MO); **San Marcos**. Between Finca El Porvenir to "Numero 6", lower South-facing slopes of Volcán Tajumulco, 1300-1500 m, 7 Mar. 1940, *J.A. Steyermark 37137* (US); **Sololá**. Pine woods bordering Rio Bravo, in vicinity of Finca Mocá, South-facing slopes of Volcán Attlán, 100 m, 21 Jun. 1942, *J.A. Steyermark 47982* (US); Sololá, above Lago de Atitlan, ½ km N of Panajachel on Highway 1, 14°45'N, 91°10'W, 1 Aug. 1965, *K. Roe & al. 767* (US); **Zacapa**. Slopes of Monte Virgen, around summit of mountain, 2200-2400 m, 12-13 Jan. 1942, *J.A. Steyermark 42603* (US).

HONDURAS. **Atlántida**. Tela, El Paguiles, Aldea San Antonio, 15°36'38"N, 87°36'04"W, 247 m, 12 Sep. 2002, *J. Pipoly 24344* (FTG); **Comayagua**. Barranco de Trincheras, 8 Aug. 1948, *L.O. Williams & A. Molina 14661* (BM, MO, US, USJ); Siguatepeque, 16 Aug. 1973, *D. Hartlett 649* (MO); Comayagua, near Cerro Trincheras, N side of highest point on road between Siguatepeque and Lago Yojoa, 991 m, 14°40'N, 87°56'W, 11 Nov. 1988, *J.M. McDougal & al. 3463* (MO); **Copán**. Between Santa Rita and Totiror Creek, 650 m, 25 Aug. 1975, *A. Molina R. 30671* (MO); **Cortés**. Mountains on north side of Lake Yojoa, 10 Apr. 1951, *C.V. Morton 7633* (US); Montaña La Cumbre, 21 Mar. 1962, *A. Molina 10566* (US); Quebrada Cusuco on Cerro Cusuco, cloud forest, 1 Aug. 1982, *W.C. Holmes 4269* (NY); **Districto Central**. Cerro La Tigra, SW of San Juancito, 1970 m, 25 Dec. 1978, *R.W. Pohl & M. Gabel 13796* (K, MO); **El Paraíso**. Mt. Yuscarán, 7 Dec. 1947, *A. Molina 620* (MO, US); **Lempira**. (Río Naranjo), Parque Nacional de Celaque, bosque nublado latifoliado alrededor el Río Naranjo y bajo el Campamento Don Tomas, 1900 m, 14°33'N, 88°40'W, 27 May 1991, *P. House 993* (MO); **Morazán**. Mt. Uyuca, 23 Oct. 1946, *L.O. Williams & A. Molina 10722* (MO, US); Mt. Uyuca, 17 Jul. 1948, *S.F. Glassman 1947* (NY); N of Mt. Uyuca, caminos Tatumbla, Labranza y Quebrada El Granadillo, sobre Mt. Uyuca, 4 Nov. 1948, *A. Molina 1432* (US); Region of El Jicarito, above Zamorano, above Aqua Amarilla, along Río Triquilapa, 26 Sep. 1950, *P.C. Standley 26837* (US); Mt. Uyuca, 19 Oct. 1951, *J.R. Swallen 10904* (MO, US); San Antonio del Oriente, 20-21 Oct. 1951, *J.R. Swallen 10973* (MO, US); Cloud forest, Mount Uyuca, 1500-1800 m, Aug. 1960, *H.W. Pfeifer 1414* (US); Mt. Uyuca near Zamorano, 29 Jan. 1964, *H.S. MacKée 11284* (P, US); Zamorano near Tegucicalpa, vicinity of Escuela Agricola Panamericana, 1966, *G.F. Freytag 319* (MO); Quebrada El Chorrito, Cerro de Hule 20 km S of Tegucigalpa, 1968, *A. Molina 18494* (BM, NY); Cerro Uyuca, ca. 8 km W of El Zamorano, 1670 m, 16 Jun. 1970, *G. Davidse & R.W. Pohl 2098* (MO); Cerro La Tigra, ca. 10 km NE of Tegucigalpa, 17 Jun. 1970, *G. Davidse & R.W. Pohl 2119* (MO, US), **n = 18!** (Davidse 1978); Between San Juancito & Valle de Angeles, 17 Jun. 1970, *G. Davidse & R.W. Pohl 2126* (K, MO, NY, US); 29 km from Tegucigalpa along road to El Zamorano and Danli, 1400 m, 8 Oct. 1975, *G.E. Pilz & M. Pilz 1313* (MO); Colonia Seyapa, Tegucigalpa, 1000 m, 4 Nov. 1981, *F. Espinal 112* (MO); Enredadera, balneario San Matias, 20 km al N de Tegucigalpa, 25 Sep. 1983, *M.E. Lara 60* (MO); **Ocotepeque**. At edge of forest El Portello on Cordillera Meredon, 20 km from Nueva Ocotepeque, 28 Aug. 1968, *A. Molina 22361* (G, MO); Aldea de Belen Gualcho y alrededores, 40 km al E de Nueva Ocotepeque, 29 Jun.-03 Jul. 1976, *C. Nelson & al. 3648* (MO); Ocotepeque, 15 Apr. 1977, *C. Nelson & al. 4034* (BM); **Santa Barbara**. Lake Yoja, 7 Aug. 1948, *L.O. Williams & A. Molina 14517* (BM, US); El Mochito, 1000 m, 29 Jun. 1970, *G. Davidse*

& R.W. Pohl 2209 (MO, US); Santa Barbara, Trinidad, Finca Las Colmenas, 480 m, 22 Jun. 1982, *J. Leonel Salguero 11* (MO); **Yoro**. Río Pijol Valley, 6 to 7 km S of Nueva Esperanza, 1570-1670 m, 15°12'N, 87°35'W, 27 May 1993, *R.L. Liesner 26580* (MO).

MEXICO. **Alta Verapaz**. A 2 km al S de Jolomylix, Teleman, Panzos, Sierra de Las Minas, 750 m, 20 Jul. 1988, *M. Esteban & al. 22885* (MO); **Chiapas**. Mt. Ovando, 15-18 Nov. 1939, *E. Matuda 3987* (NY); Km 1134, Pan-American Highway, 4 Jun. 1950, *J.T. Baldwin Jr. 14342* (US); Above canyon El Sumidero, N of Tuxtla Gutierrez, 7 Oct. 1953, *N.C. Fassett 29100* (US); Sierra Madre, near Mapastepec, 3 Nov. 1960, *T. Tateoka 1003* (US); Tuxtla Gutierrez, 10 Nov. 1960, *T. Tateoka 1004* (US); Tenejapa, along the Ala Shashib River above Habenal, paraje of Mahben Chauk, 14 Jul. 1964, *D.E. Breedlove 6428* (US); Venusiano Carranza, 3 miles S of Aguacatenango along road to Pinola Las Rosas, 13 Oct. 1965, *D.E. Breedlove & P.H. Raven 13121* (NY, US); 3 miles S of La Trinitaria, 14 Oct. 1965, *D.E. Breedlove & P.H. Raven 13208* (US); Ocozocoautla de Espinosa, 19 km N of Ocozocoautla along road to Mal Paso, 28 Oct. 1965, *D.E. Breedlove 13956* (NY); Zinacantàn, 7 Jul. 1966, *R.M. Laughlin 1218* (NY); Tenejapa, in the paraje of Mahosik', 8 Aug. 1966, *D.E. Breedlove 14829* (US); Along Mexican Highway 190 at the Zinacantàn paraje of Muctajoc, 18 Aug. 1966, *R.M. Laughlin 1572* (US); Tenejapa, moist slope with *Quercus*, *Pinus*, *Nyssa* and *Liquidambar*, in the paraje of Mahosik', 12 Sep. 1966, *A.S. Ton 1183* (NY); Ixtapa, along Highway 190 at the Zinacantàn paraje of Muk'tahok', 3 Oct. 1966, *R.M. Laughlin 2289* (US); El Zapotal, along trail from Zinacantàn paraje of Pasté to San Lucas, 20 Oct. 1966, *R.M. Laughlin 2553* (US); Tenejapa, along a small river in the barrio of Tih Ha', paraje of Mahbenchauk, 28 Oct. 1966, *A.S. Ton 1446* (NY, US); Tenejapa, slope with *Quercus* and *Pinus* in the paraje of 'Oshewits', 22 Nov. 1966, *A.S. Ton 1582* (NY, US); Acala, wooded slope along the Rio Grijalva, 10 km S of Mexican Highway 190, along the road to Acala at Nandaburri, 24 Nov. 1966, *R.M. Laughlin 2807* (US); Berriozabal, 6-8 km N of Berriozabal near Pozo Turipache and Finca El Suspiro, 10 Oct. 1971, *D.E. Breedlove 20352* (NY); 17,5 km on the road to Mal Paso from Ocozocoatla, 31 Jul. 1972, *H. Kennedy 1398* (US); Cintalapa, SE of Cerro Baul on the border with the State of Oaxaca, 16 km NW of Rizo de Oro along a jogging road to Colonia Figaroa, 6 Sep. 1972, *D.E. Breedlove 27616* (NY); Ocozocoautla de Espinosa, 18-20 km N of Ocozocoautla along road to Mal Paso, 27 Sep. 1972, *D.E. Breedlove 28156* (NY); Tuxtla-Gutierrez, pressi de La Coyota, 18 Oct. 1974, *R. Bavazzano s.n.* (FT); Ca. 8 miles NE of Solistohucan along Highway 195 between Villa Hermosa and Tuxtla Guttierez, 1800 m, 10 Aug. 1975, *G. Davidse & J. Davidse 9458* (US), **n = 18!** (Davidse 1978); 30 miles W of San Cristobal de Las Casas on Highway 190, 13 Oct. 1976, *J. Brunken & C. Perino 348* (US); 67 km from Route 190 toward Ocosingo, 1290 m, 6 Oct. 1984, *M.J. Huft & E. Cabrera 2373* (MO); Tuxtla Gutierrez, El Zapotal, 25 Dec. 1984, *C. Cowan 5033* (NY); Jitotol, 7 km of Jitotol on road to Pichucalco (Highway 195), 1660 m, 17°10'N, 92°51'W, 14 Oct. 1986, *B. Hammel & al. 15696* (MO); Ocozocoautla, road Aeropuerto-Ocozocoautla-México, 19 Sep. 1988, *A. Reyes Garcías & al. 1023* (BM); Along Highway 190, 45 km N of El Jocote (empalme), 20 km from La Trinitaria, scrub forest on rocky limestone slope, 860 m, 19 Sep. 1988, *W.D. Stevens & E. Martinez S. 25750* (MO); San Cristobal de Las Casas, Ocosingo, 1 km antes del Río Chancalà, vincendo desde Palenque, 27 Sep. 1989, *M. Gonzalez-Espinosa & al. 865* (NY); 8 km from Ixtapa, 31 Jan. 1990, *P.J. Stafford & al. 138* (BM); Villacorzo, Cerro Bola, al W del ejido Sierra Morena, 1750 m, 16°8'N, 93°36'W, 3 Aug. 2002, *A. Reyes-García 5204* (MO); Ocosingo, Ejido Mariscal (antes Santa Clara), 147 m, 16°58'45"N, 91°11'7"W, 16 Feb. 2003, *D. Alvarez 3882* (MO); La Concordia, a 800 m al O del rancho Buenavista, 1640 m, 15°48'38"N, 93°03'15"W, 22 Sep. 2005, *J.M. Melendez 1066* (MO); **Colima**. Camino Juluapan-Campo Cuatro, 700–800 m, 12 Aug. 1991, *F.J. Santana & al. 5241* (US); Rancho El Jabali N of Colima in the SW foothills of the Volcán de Colima, 19°26.3'N, 103°42.5'W, 16 Sep 1991, *A.C. Sanders 11266* (K, MO); **Guanajuato**. 2-4 km E of Guanajuato, 16 Oct. 1952, *E.R. Sohns 286* (US); Ocuilan, El Ahuehuete, 30 Nov. 1969, *J. Rzedowski 26926* (US); Gentle slope of Cerro Capulin a large gentle hill just E of Mexico 43, ca. 8 km NNE of Uriangato on road to Salamanca, 1900-2100 m, 20°11'N, 101°6'W, 17 Sep. 1977, *H.H. Iltis & J.F. Doebley 128* (MO); **Guerrero**. Along main road about 10 miles N of Taxco, 6 Sep. 1959, *O. Degener & I. Degener 26291* (NY, US); Along Mex Highway 51, 17 km W of Teloloapan between km 77 and 78 at quarry, 18°25'N, 99°58'W, 22 Nov. 1971, *H.H. Iltis & T.S. Cochrane 44* (MO); La Unión, carretera Zihuatanejo-Cd. Altamirano, 34 km al NE de Vallecitos de Zaragoza, 24 Oct. 1982, *S.D. Koch & P.A. Fryxell 82171* (MO, NY); Iguala y Buenavista, Canon de La Mano entre Los Amates y El Naranjo, 10 km al N de Iguala por el ferrocarril, 900-1000 m, 13 Sep. 1986, *C. Catalan & F. Teran C. 114* (MO); **Hidalgo**. NW of Lake Atexca, 9 Nov. 1946, *H.E. Moore 1951* (US); Metztitlan, between Cerro Colorado, and head of descent into Barranca de Metztitlan on road from Pachuca to Zacualtipan, 31 Jul. 1948, *H.E. Moore 4235* (US); Puerto del Zopilote, 22 Sep. 1949, *H.E. Moore 5076* (BM, G, US); **Jalisco**. San Nicolas, 25 Sep. 1910, *A.S. Hitchcock 7207* (US); Guadalajara, La Barranca, 17 Nov. 1930, *M.E. Jones 27414* (MO); Near El Molino, about 25 miles SW of Guadalajara, 2 Oct. 1952, *R. McVaugh 13306* (G, K, US); Mountain summits 9-10 miles SE of Autlan, 1300-1600 m, 16 Nov. 1952, *R. McVaugh 14232* (US); Barranca of Río Verde, ca. 20 km N of Tepatitlán on road to Yahualica, 27-28 Aug. 1958, *R. McVaugh 17363* (G, NY, US); Above the west end of Lake Chapala, Midway between Jocotepec and S. Juan Cosalá, precipitous rocky south-facing mountainsides and barrancas, 8 Nov. 1959, *R. McVaugh & W.N. Koelz 360* (G); 10-16 miles NE of Autlàn, on the cuesta above the river bridge at El Corcovado, 2 Oct. 1960, *R. McVaugh 19756* (NY); Jalisco, 40 km al SWS de Guadalajara, El Molino, cerca de Huejotitàn, 2 Nov. 1960, *J. Rzedowski 14254* (US); Los Lles, 29 Sep. 1980, *A.A. Beetle 5925* (MO); Purificacion, 15.3 km SW of Autlan de Navarro on Highway 80, 8 Oct. 1985, *B. Bartholomew 2769* (NY); Tuxcacuesco, Cerro del Palacio, 5–6 km al WSW de Tuxcacuesco, 5–6 km al ENE de Zenzontla, 1150 m, 18 Oct. 1991, *F.J. Santana & B. Benz 5369* (US); **México**. Temascalpetec, 10 Sep. 1932, *G.B. Hinton 1909* (K, NY, US); Temascalpetec, Limones, 10 Jul. 1934, *G.B. Hinton 6722* (BM, K, MO, NY, US); Jilotepec, 21 Sep. 1952, *E. Matuda 26752* (MO); Ixtapan, 2 km N of Ixtapan at km 145 on Highway 55, 18°50'N, 99°25'W, 9-10 Sep. 1965, *K. Roe & E. Roe 1903* (US); **Michoacán**. Vicinity of Morelia, 26 Aug. 1909, *F. Arséne 2976* (BM, NY, US); Rincón près Morelia, 8 Sep. 1910, *F. Arséne 31* (G, L, US); Morelia, 8 Sep. 1910, *F. Arséne 5287* (K, MO, NY); Vicinity of Moreila, 2 Jun. 1912, *F. Arséne 8487* (MO, US); Apatzingán, Anguilla, 9 Dec. 1939, *G.B. Hinton 15156* (MO, NY, US); Below Tecámbero on road to Chipio, 10 Nov. 1949, *H.E. Moore & al. 5598* (BM, G, US); Lower north facing slopes of Cerro Santa Maria, in grassland with occasional shrubs, 8-10 km, SW of Jiquilpan and 5 km NE of Quitupan, 5-7 Aug. 1959, *C. Feddema 131* (NY, US); West facing slopes of Cerro de Carboneras above the Rio Cupatitzio, ca. 22 km S of Uruapan, 16-22 Oct. 1961, *R.M. King & T.R. Soderstrom 4813* (NY, US); Ca. 1.7 mi. NW of Tuxpan, 19 Aug. 1975, *G. Davidse & J. Davidse 9819* (K, MO, NY, US), **n = 18!** (Davidse

1978); 1.2 miles E of Tuxpan on Mex. 15, 1879 m, 20 Oct. 1976, *J. Brunken & C. Perino 440* (MO); Aquila, 5 km carretera La Placita-Tecoman, 31 Aug. 1979, *B. Guerrero 275* (NY); Ixtlán, Comaltepec, La Esperanza, 1600 m, 17°37'N, 96°21'W, 27 Jul. 1989, *R. López Luna 493* (MO); **Morelos**. Barranca près Cuernavaca, 14 Nov. 1865, *E. Bourgeau 1299* (P); Near Cuernavaca, 21 Aug. 1897, *C.G. Pringle 6663* (G, K, MO, NY, P, US, W); **Nayarit**. Tepic, vicinity of Acaponeta, 11 Apr. 1910, *J.N. Rose & al. 14459* (NY); Mountains 10 miles SE of Ahuacatlan, on the road to Barranca del Oro and Amatlán, 17-18 Nov. 1959, *R. McVaugh & W.N. Koeltz 828* (US); Ahuacatlán, 10 km al S de Ahuacatlán, camino a Amatlán de Cañas, 21°00'N, 104°30'W, 19 Oct. 1986, *O. Téllez 9882* (MO); Km 2-5 por el camino del Cangrejo a la Mesa del Nayar por la barranca, en la caras S y E de la montaña, 1100 m, 22°14'N, 104°39'W, 17 Sep. 1989, *O. Tellez V. 12194* (MO); **Nuevo León**. Mina Gro., Manchon, 25 Sep. 1936, *G.B. Hinton 9581* (BM, K, MO, NY, W); Mina, Chilacayote-Mangito, 30 Nov. 1939, *G.B. Hinton 14932* (NY); Villa Santiago, trail between Potremo Redondo and Las Ajuntas, 24 Aug. 1939, *C.H. Muller 2961* (MO, US); **Oaxaca**. s.d., *H. Galeotti 5725* (W); Mirador, Jul. 1841, *F.M. Liebmann 6317* (C, L, MO, NY); Tomellin Canyon, 17 Jul. 1897, *C.G. Pringle 6701* (BM, G, K, P, MO, NY, US, W); Alturas San Pablo Arritzo, 25 Aug. 1897, *C. Conzatti 2012* (US); Cafetal Montecristo, 30 Sep. 1917, *B.P. Reko 3474* (US); Ubero, Jun. 1937, *L.O. Williams 9468* (G, US, W); Cañon of the Rio Zavaleta near the village of San Pablo Quatro Venados 15-18 km WSW of Oaxaca, 20-25 Jan. 1937, *W.H. Camp 2461* (MO); 24 Aug. 1974, *J. Conrad & R. Conrad 3064* (K, L, MO); Along Highway 175 through Sierra de Juarez between Tuxtepec and Oaxaca, 1400 m, 19 Feb. 1979, *T.B. Croat 48019* (MO); Near San Miguel de Tlacotepec at San Antonio Tonuchi, 22 Jun. 1980, *A.A. Beetle 4617* (MO); Ca. 4 miles E of San Juan Coatzospan, 31 Jan. 1981, *J. Bauml & M. Kimnach 453* (US); Juchitan, "Arroyo Pita", 23 km al N de Lazaro Cardenas, brecha a Santa Maria Chimalapa, 320 m, 14 Mar. 1983, *P. Tenorio & al 3503* (MO); Ixtlàn, Sierra de Juarez, ruta 175 Tuxtepec a Oaxaca, 5 km al NE de Vista Hermosa, 28 May 1983, *R. Cedillo 2351* (US); 97 km by road S of Teotitlán on road to Oaxaca, 10 Oct. 1983, *W.R. Anderson 12995* (MO, NY); 8 km W of Chiapas border on Highway 190, 19 Oct. 1983, *W.R. Anderson 13221* (MO, NY); Ixtlan de Juarez, rio que pasa por San Pedro, sobre la carretera Ixtlan-Zoogucho, 19 Jul. 1985, *M. Gonzalez L. & al. 166* (MO); Totopalan, 3 km de Portello San Dionisio, carretera Oaxaca-Iehuantepec, 29 Jun. 1987, *G. Manzanero 1141* (NY); Ixtlan, Santiago Comaltepec, Puerto Eligio, 17°45'N, 96°30'W, 8 Dec. 1987, *E. López Garcia 56* (MO, NY); 28.2 km NE of Ojo de Agua on MEX Highway 131 towards Oaxaca, 1750 m, 7 Sep. 1990, *P. Peterson & al. 9819* (FT, US); Tlaxiaco, San Pedro Molinos, km 64 carretera Tlaxiaco-Putla, 17°13'0"N, 97°43'04"W, 16 Oct. 1994, *J.L. Panero 5060* (MA, NY); Ixtlan de Juarez, 2 Aug. 1999, *J. Garcia R. 388* (MO); Santiago Chazumba, 20 Nov. 2005, *J.I. Calzada 24618* (K); **Puebla**. At and near the summit of El Cerro de Cuhuatepetl, Tehuacan, 31 Aug. 1944, *J.V. Santos 3347* (US); Caltepec, ladera N de la Mesa de Pala, al SE de Acatepec, 2180 m, 14 Aug. 1984, *P. Tenorio & al. 6899* (MO); Tlatlauquitepec, 7 Oct. 1998, *E. Contreras 5972* (K); **San Luis de Potosí**. Las Canoas, 15 Aug. 1891, *C.G. Pringle 3808* (BM, G, K, NY, P, US, W); San Luis Potosí, Jul. 1911, *C.A. Purpus 5440* (NY); Between Puerta Huerta and Rioverde in the Sierra de Alvarez, 11 Sep. 1954, *E.R. Sohns 1198* (K, P, US); In the Sierra de Guadalcazar between Charco Blanco and Aguaje de Garcia, 20 Sep. 1954, *E.R. Sohns 1378* (K, US); San Luis de Potosí, in the Sierra de Alvarez along the route, Cerritos-La Joya-Montaña-Villar, 21 Sep. 1954, *E.R. Sohns 1390* (K, US); 34 miles E of San Luis Potosí on the Rioverde Highway, Sierra de Alvarez, 6 Nov. 1960, *M.C. Johnston 6028* (US); S13 km W of Santa Catarina on Highway 86 at km 58, 22°05'N, 100°35'W, 29 Sep. 1965, *K. Roe & E. Roe 2207* (US); 41 miles W of San Luis Potosí on the road to Rioverde, 20 Oct. 1966, *J.R. Reeder & C.G. Reeder 4765* (US), **n = 18!** [Reeder 1968 as *L. sloanei* (Griseb.) Hitchc.]; **Sinaloa**. Along the road to Micro Ondas la Palma, 6 Oct 1975, *J.L. Reveal & R.M. Harley 4020* (K, NY); **Tabasco**. Tenosique, a 15 km arriba de la palma por rio a 5 km del Rancho Punta de Montaña del Sr. Angel Zubieta, 4 Jul. 1981, *C. Cowan 3374* (NY); **Tamaulipas**. 22 km SE of Miquihuana, 12 Aug. 1941, *L.R. Stanford & al. 870* (MO, NY); En route to Pena Nevada out of Hermosa, 16 Jul. 1949, *L.R. Stanford & al. 2502* (US); Gomez-Farias, environs de Casa de Piedra, 1400 m, 9 Aug. 1969, *H. Puig 5167* (P); **Veracruz**. Orizaba, Aug. 1854, *M. Botteri 149* (BM); Córdoba, 21 Feb. 1866, *E. Bourgeau 1936* (P, US); Orizaba, 12 Jul. 1866, *E. Bourgeau 2648* (G, L, K, NY, P, US); La Luz prés de Córdoba, 2 Oct. 1882, *E. Kerber 74* (BM, C, G, P, UPS); Orizaba, Cordoba, 20 Aug. 1891, *H.E. Seaton 393* (NY); Zacuapan, Nov. 1908, *C.A. Purpus 3779* (NY, US); Veracruz, 25 Aug. 1910, *A.S. Hitchcock 415* (BM, C, G, K, L, MO, NY, P, US, W); Córdoba, 27 Aug. 1910, *A.S. Hitchcock 409* (G, K, L, MO, NY, US, W); Near Coatepec, 2-4 Sep. 1910, *A.S. Hitchcock 6680bis* (US); Orizaba Temascalpetec, Tejupilco, 10 May 1933, *G.B. Hinton 4958* (BM, K, NY, W); Near San Martín, 1933, *H.W. von Rozynski 589* (G, NY); Cordoba, 28 Jul. 1935, *G.L. Fisher 35298* (MO, NY); From El Rancho de Sacatalica to El Municipio de Zongolica, 23-25 Jun. 1944, *J.V. Santos 3076* (NY, US); Along the Trans-Isthmian Highway (route 185), 4 km NE of Minatitlàn, 3 Aug. 1958, *R.M. King 1057* (US); Orizaba, Cerro de Cuauhtlapan, 26 Nov. 1967, *M. Rosas 830* (BM, P, UPS); Near Jalapa, La Pyramida de Macuiltepec, 12 Dec. 1972, *A.A. Beetle 2216* (MO); Sierra San Cristobal between Ciudad Mendoza and Orizaba, along autopista ca. 3 km SW of Orizaba, S of autopista ca. ½ km, 1260-1400 m, 27 Jun. 1977, *T.B. Croat 39510* (MO); Huatusco, Dos Puentes, carretera Huatusco-Totutla, 19°12'N, 96°57'W, 11 Jul. 1979, *S. Avendano & al. 351* (NY); Near "La Calavera", 10 km N of Altotonga, 19°51'N, 97°13'W, 28 Jun. 1980, *M. Nee & B.F. Hansen 18645* (BM, MO); Soteapan, along trails to base of Volcán Santa Marta, 0-3 km E of village of Santa Marta, 1100-1200 m, 18°21'N, 94°52'W, 29 Jun. 1982, *M. Nee & al. 24676* (MO); Rio Blanco, a 1 km de Rio Blanco por el camino a El Cerro del Cristo, 1250 m, 18 Jul. 1984, *H.M. Hernández & A. Chacón 479* (MO); Gutierrez Zamora, E of Rio Tecolutla and S of Highway Mex. 180, 3 km E of Gutierrez Zaora, 20°25'N, 97°04'W, 19 Aug. 1986, *M. Nee 32791* (MO, NY); Soteapan, 6 km al NE de Ocotal Chico, 13 Jul. 1987, *R. Acosta & L. Ceja 1652* (NY); 1.4 miles N on Mex 125 from its junct. with the road to Ixhuatlan, S of Huatusco, 10 Jul. 1990, *S. & G. Jones 5385* (NY); El Esquilon, on the road from Xalapa to Naolinco de Victoria, 09°65'W, 19° 39'N, 7 Nov. 1993, *M. Sparrow & P. Brewster 27* (K); **Yucatán**. 3 km al W de Koncal, 21°06'N, 89°42'W, 16 Oct. 1993, *L. Rico 1177b* (NY, US).

NICARAGUA. **Carazo**. Jinotepe, 3-7 Nov. 1911, *A.S. Hitchcock 8665* (BM, K, NY, US); **Estelí**. Reserva Natural Miraflor, Comarca de Sontule, 1050-1200 m, 13°12'N, 86°20'W, 8 Jul. 1999, *R. Rueda & al. 115551* (MO); Miraflor, 910 m, 13°12'43"N, 86°19'50"W, 13 Oct. 2007, *R.A. Rugama 22* (MO); **Granada**. Volcán Mombacho, 1400 m, 11°50'N, 85°57'W, 11 Jan. 1981, *W. Hahn 374* (MO); **Jinotega**. La Bastilla, 10 km NE of Jinotega, 11 Jan. 1969, *F.C. Seymour 2120* (MO); Along Lago Apanas, near Jinotega, 1000 m, 4 Dec. 1973, *L.O. Williams & A. Molina R. 42756* (MO); Along Highway 3 ca. 1.9 km NW of Aranjuez road entrance, 1460-1480 m, 13°02'N, 85°56'W, 31 Oct. 1982, *W.D. Stevens 21913*

(MO); Wiwili, zona de Amortiguamiento de Bosawas, macizos del Cerro Kilambè, 13°33'N, 085°41'W, 10 Aug. 1998, *R. Rueda & al. 8475* (MO); Reserva Natural Kilambé, Comarca Aguas Rojas, 13°22'N, 085°41'W, 18 Mar 2001, *R. Rueda & al. 15800* (BM, MO); **Madriz**. Cerro Volcán de Somoto (Tepesomoto), cerca la cima, 1500-1600 m, 13°25'N, 86°34'W, 16 Apr. 1980, *P.P. Moreno 2145* (MO); **Managua**. Casa Colorada and vicinity, 850 m, 27 Jun. 1923, *W.R. Maxon & al. 7408* (US); Río Las Nubes, Feb. 1936, *A. Garnier 1549* (US); Ca. 0.6 km from 2 (Carretera Sur) on road along ridge of Sierra de Managua from Highway 2 to Highway 12 (Carretera vieja a León), near El Pescado, 800 m, 12°00'N, 86°19'W, 19 Oct 1977, *W.D. Stevens & al. 4730* (MO); **Masaya**. Miravalle, a 4 km de Las Nubes, 700-800 m, 12°00'N, 86°16'W, 11 Dec. 1980, *P.P. Moreno 5185* (MO); **Matagalpa**. Sta. María de Ostuma, 8-15 Jan. 1963, *L.O. Williams & al. 23340* (G, NY, US, W); Cloud forest area about 5 km N of Matagalpa, Cordillera Central de Nicaragua, 13 Jan. 1963, *L.O. Williams & al. 23739* (US); Between Matagalpa and Jinotega, 8-15 Jan. 1963, *L.O. Williams & al. 23316* (G, NY, US, W); Matagalpa, N of Santa Maria de Ostuma, 28 Nov. 1973, *L.O. Williams & A. Molina 42666* (BM, US); Matagalpa, El Ocotal, 4 km al S de la ciudad de Matagalpa, 900-1000 m, 12°52'N, 85°55'W, 5 Oct. 1982, *P.P. Moreno 17664* (MO); Behind La Selva Negra Hotel, slopes of Cerro Picacho, near the border with Dept. Jinotega, 1200-1540 m, 13°00'N, 85°55'W, 23-25 May 1985, *G. Davidse & al. 30443* (MO); **Nueva Segovia**. Jalapa, Cerro de Jesús, 1255-1660 m, 13°58'50"N, 86°10'54"W, 17 Jul. 2006, *D. Paguaga 4* (MO); **Rivas**. Isla Omotepe, Volcán Maderas, 800-1200 m, 11°26'N, 85°30'W, 19 Sep. 1984, *W. Robleto 1151* (MO).

PANAMA. **Bocas del Toro**. Along trail on divide separatine Chiriquí and Bocas del Toro, 08°45'N, 82°15'W, 1150 m, 22 Oct. 1985, *G. MacPherson 7220* (MO, PMA); Bocas del Toro, Cerro Colorado, ca. 8.6 miles W of Chamé, ca. 3 miles beyond junction of road which goes S to old construction camp for copper ore exploration, along trail N of divide toward Atlantic slope which leads down a rocky stream, 1450-1480 m, 8°35'N, 81°50'W, 7 Jul. 1988, *T.B. Croat 69119* (MO); **Chiriquí**. Cerro Vaca, E of Chriquì, 25-28 Dec. 1908, *H. Pittier 5331* (NY, US); Vicinity of El Boquete, 28 Sep.-7 Oct. 1911, *A.S. Hitchcock 8269* (US), *8270* (NY, US), *8286* (US), *8311* (US), *8315* (US); Boquete, 29 Mar. 1938, *M.E. Davidson 710* (MO, US); Vicinity of Boquete, Finca Collina, 5800-6700 ft, 13 Mar. 1963, *W.L. Stern & al. 2032* (MO, US); Vicinity of Boquete, 12-13 Dec. 1966, *W.H. Lewis & al. 569* (K, MO, NY, US); Along road between Boquete and Cerro Horqueta, scandent grass, fruits green, 2 Aug. 1967, *J.A. Duke 13704(4)* (MO, SCZ); Chiriquí, 1.5 miles W of Cerro Punta, valley of Río Chiriquí Viejo, 20 Jan. 1968, *S. McDaniel 10158* (NY, US); N of San Felix at Chiriquí-Bocas del Toro border, on Cerro Colorado, copper mine road along continental divide, lower montane rain forest, 5 May 1975, *S. Mori & J. Kallunki 5916* (MO, US); E slope of Volcán de Chiriquí (Barú) WNW of Boquete, 19 Nov. 1975, *G. Davidse & W.G. D'Arcy 10155* (K, MO, US), **n = 18!** (Davidse 1978); NE del campamento de Fortuna (Hornito), 08°45'N, 82°15'W, 26 Sep. 1976, *M. Correa & al. 2869* (K, MO, NY, PMA, US); 10 km N of Los Planes de Hornito, 1150 m, 18 Jun. 1982, *S. Knapp & M. Vodicka 5623* (MO); Vicinity of Fortuna Dam, along Quebrada Arena, just south of continental divide, 1050 m, 8°45'N, 82°15'W, 8 Sep. 1987, *G. McPherson 11692* (MO); Large meadow adjacent to Río Caldera just N of Boquete, 1060 m, 9 Mar. 1989, *P.M. Peterson & C.R. Annable 7382* (MO); Near Costa Rican border, 13 km by road S of Río Sereno, Finca Hartmann, 1800 m, 8°50'N, 82°45'W, 13 May 1991, *N. Hensold & G. McPherson 1035* (MA, MO, NY, PMA); Near Costa Rica border, 1550-1750 m, 08°50'N, 82°45'W, ca. 13 km from Río Sereno, 23 Oct. 1992, *G. McPherson 15958* (BM, MO, PMA); Finca de la Familia Herrera, 5 Nov. 1994, *R. Castello 47* (US); Chiriquí, Pietra Candela, 18 May 1996, *M. Ramirez 98* (PMA); Bajo Morro (Boquete), 8°48'18"N, 82°26'96"W, 1319 m, 4 Oct. 2009, *A. Goméz 99* (PMA); Reserva Forestal Fortuna, sendero al E del Centro para la ICBT, 8°43'59"N, 82°14'16"W, 1110 m, 20 Jan. 2012, *M.N.S. Stapf & R.M. & Baldini 858* (FT, PMA, SCZ); Bugaba, orillas de la carretera entre Bijao y Volcán, 8°43'54"N, 82°37'32"W, 1201 m, 22 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 867* (FT, PMA, SCZ); Chiriquí, Volcán, carretera a Aguacatal, SW del Volcán Barú, 8°47'36"N, 82°34'54" W, 2079 m, 23 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 871, 872, 874, 875, 878* (FT, PMA, SCZ); Carretera Volcán-Río Sereno, Puente sobre el Río Chiriquí Viejo, 8°48'27"N, 82°40'W, 1338 m, *M.N.S. Stapf & R.M. Baldini 897* (FT, SCZ); Carretera Boquete-Palo Alto, 847'43"N, 82°26'26"W, 1227 m, 24 Jan 2012, *M.N.S. Stapf & R.M. Baldini 900* (FT, PMA, SCZ); Reserva Forestal Fortuna, primer puente despues de la Estación Biologica del STRI, 8°44'02"N, 8215'02"W, 1307 m, 10 Jul. 2012, *O.O. Ortiz & al. 776* (PMA); Reserva Forestal Fortuna, Hornito, Valle La Mina, hacia Pueblo Nuevo, 8°39'26"N, 82°12'54"W, 1174 m, 2 Feb. 2014, *O.O. Ortiz & R.M. Baldini 1989* (FT, PMA); **Coclé**. 5 km W of El Valle, 3000 ft, 26 Feb. 1978, *B. Hammel 1765* (MO); Bugaba, Santa Clara, 08°50'N, 82°44'W, seasonally dry forest near Santa Clara, 1 Mar. 1985, *H. van der Merff & J. Herrera 7316* (MO, PMA); **Darién**. Darién, Cerro Sapo, 2500 ft, 1 Feb. 1978, *B. Hammel 1209* (MO); Trail along ridge S of Río Setigandi, almost on Colombian border, 700-1000 m, 21 Apr. 1980, *A. Gentry & al. 28731* (MO, PMA); Serranía de Canazas, Reserva privada Chucantí, Cerro Chucantí, 8°47'45"N, 78°27'47"W, 1325 m, 29 Aug. 2014, *O.O. Ortiz & al. 2446* (FT, PMA); **Panamá**. Canal Zone, 1 mile N of Madden Dam on the Colon Highway, edge of "*higher forest*", 30 Apr. 1969, *R.L. Lazor 2945* (SCZ); Majé, up Río Majé about 5 miles, steep forested ridge above Chocó Indian trail, 18 Nov. 1970, *H. Kennedy & R. Foster 677* (NY); Canal Zone, along road to Gamboa airport, 13 May 1971, *T.B. Croat 14603* (NY); Altos de Campana, Monte Sulin, 3 Dec. 1977, *R. Mendez 98* (PMA); Parque Nacional Altos de Campana, carretera a Chica', 8°40'29"N, 79°55'45"W, 798 m, 14 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 813* (FT, PMA, SCZ); **Veraguas**. Río Segundo Brazo, 8 Sep. 1974, *P.J.M. Maas & R.L. Dressler 1635* (K, MO, NY); Trail up E side of Cerro Tute, 1200 m, 25 Oct. 1975, *J.T. Whitherspoon & al. 8866* (MO); Mountains W of Alto de Piedras Junior High School N of Santa Fé, slopes and peak of Cerro Arizona, 300-4700 ft, 11 Sep. 1978, *B. Hammel 4701* (MO); Mountains of southern Azuero Peninsula Los Santos, near proposed route of road from El Cortezo to Arenas, ca. 10 km SW of El Corezo, 1500-3800 ft, 27 Oct. 1978, *B. Hammel 5370* (MO); Veraguas, Cerro Tute, W of Santa Fé, beyond Alto da Pedra, 08°30'N, 81°7'W, 600-800 m, 17 Oct. 1985, *G. MacPherson 7179* (MO, PMA); Soná, Bahía Honda, entre Playa del Sol y Salmonete, intorno del Río Luis, 7° 48'N, 81° 35'W, 5 Jul. 2001, *S. Castroviejo & al. s.n.* (MA, PMA); Santa Fé, Alto de Piedra, camino hacia Cerro Tute en las faldas del Cerro Mariposa, 8°30'35"N 8106'57"W, 858 m, 19 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 847, 849* (FT, PMA, SCZ).

PERÚ. **Amazonas**. Chachapoyas, Leimebamba-Chilchos trail, 2 Jul. 1977, *J.D. Boecke 2095* (MO, NY); Bagua, 12 km E of La Peca, 9 Jul. 1978, *P.J. Barbour 2693* (MO, NY); Bongara, traila bove Highway to Chiclayo and Río Utcubamba, 3-10 km NW of Pedro Ruiz Gallo, ca. 1300-1400 m, 4 May 1981, *K. Young & M. Eisenberg 293* (MO); **Cajamarca**. Santa Cruz, Catache, upper Río Zaña, ca. 5 km above Monte Seco on path to Corro Blanco, 1500-

2000 m, 16-18 Mar. 1986, *M.O. Dillon & al. 4360* (MO, NY, US); Jaen, Colasay, 1600 m, 05°55'00"S, 79°10'00"W, 8 Dec. 2001, *R. Vasquez & al. 27196* (MO; **Cuzco**. Urubamba, ruinas de Machu Picchu, a ca. 112 km de Cuzco, en el camino ferroviario Cuzco-Quillabamba, 2000 m, 24 Mar. 1987, *P. Nuñez 7545* (MO); Paucartambo, Kosñipata Valley, km 150, San Pedro, Río Union and Río Kosñipata junction, 800 m, 20 Mar. 1990, *P. Nuñez 11946* (MO); **Oxapampa**. Villa Rica, Centro poblado, Palma (Centro Bocaz), Camino a Alto Atarraz, 1515 m, 10°39'17"S, 75°11'35"W, 14 Jan. 2005, *L. Franco Mellado & al. 2559* (MO); **San Martín**. Rioja, montane forest along road Rioja-Pedro Ruiz, 1350 m, 25 Mar. 1998, *H. van der Werff & al. 15616* (MO).

VENEZUELA. **Aragua**. Tovar, 29 Aug. 1855, *A. Fendler 1619* (K, MO); Aragua, high pass between Chroní and Maracay, 6500 ft, 5-6 Apr. 1962, *T.R. Soderstrom 974* (MO, NY, P, US); Near Maracay, Parque Nacional Rancho Grande, near field station, 8 Jun. 1967, *T.R. Soderstrom 1357* (US); Parque Nacional Henry Pittier NW of Maracay, Rancho Grande, 1150 m, 13 Nov. 1971, *G. Davidse 3033* (MO, US), **n = 18!** (Davidse 1978), *3038* (MO); High pass Aragua, Alto de Coroni, ca. 28 km N of Maracay, 1500 m, 14 Nov. 1971, *G. Davidse 3100* (L, MO, US), **n = 18!** (Davidse 1978); Cordillera Interior, faldas que miran al N a lo largo del camino entre El Pauji y El Socorro, hacia la represa, al S de El Consejo, 1350-1400 m, 10°11'N, 67°15'W, 16 Jul. 1979, *J.A. Steyermark & A. Stoddart 118178* (MO); Parque Nacional Henri Pittier, along the road from Maracay to Coroni, 1595-1640 m, 11 Nov. 1984, *A.L. Weitzman & B.M. Boom 145* (MO, NY, US); **Bolívar**. Savannas vicinity of Mission Santa Teresita de Kavanayén, 1200-1300 m, 11 Dec. 1952, *B. Maguire & J.J. Wurdack 33758* (NY, US); **Districto Federal**. Umgebung von Maracay und Caracas, 1930-1934, *P.C. Vogl 944* (G); Sabana de Cortina, 11 Mar. 1940, *A. Chase 12408* (US); Districto Federal, S and SW facing densely wooded slopes of Cordillera del Avila, above Caracas, between Los Venados and Papelon, 1585-1820 m, 30 Dec. 1943, *J.A. Steyermark 55106* (US); Caracas, La Guaira, 23 Jun. 1946, *A. Burkart 17001* (K); Cerro Naiguatá, laderas pendientes del lado del mar que miran hacia el Norte, arriba del pueblo de Naiguatá, bosque humedo denso, Lomas de Las Delicias, entre Quebrada de Basenilla y Quebrada Guayoyo, 9-12 km SE de Hacienda Cocuizal, 1000-1300 m, 15-19 Nov. 1963, *J.A. Steyermark 92125* (US); Between El Junquito and Colonia Tovar, 2100 m, 27 Oct. 1972, *J.J. & M.L. Wurdack 2674* (US, VEN); Districto Federal, intersection road between El Junquito and Tovar and road to Carayaca, 1770 m, 13 Nov. 1973, *G. Davidse 3999* (K, MO), **n = 18!** (Davidse 1978), *4032* (MO, US); Capital, Libertador, Parque Nacional Waraira Repano (El Ávila), 10°30'55"N 66°53'09"W, 1090-1150 m, 3 Dec. 2015, *R. Gonto et al. 6633* (NY); **Falcón**. Sierra de San Luis, Montaña de Paraguariba, 23 Jul. 1967, *J.A. Steyermark 99450* (NY); Sierra San Luis, Paraguariba, ca. 2-3 km NNE de la cumbre del Cerro Galicia, 1300 m, 24 Feb. 1985, *R. Wingfield 13695* (MO); **Lara**. Jiménez, hills along road between Alto del Viento to Cerro Pando, 1000-1700 m, 69°34'W, 9°39'N, 26 Oct. 1982, *G. Davidse & A.C. González 21206* (MO, NY); **Mérida**. Rich forest above Hacienda Agua Blanca, above La Aulita, 1375-1920 m, 25 Apr. 1944, *J.A. Steyermark 56098* (US); 66 km NE of Merita along Merita-Azulita road, 1900 m, 20 Nov. 1971, *G. Davidse 3240* (L, MO, NY, US), **n = 18!** (Davidse 1978); Elfin Forest, Estanques-Paramos de los Colorados, 12 Mar. 1980, *G.L. Sobel & J. Strudwick 2155* (MO, NY); Libertador, vía al Páramo de la Culata, 08°39'12"N, 71°07'57"W, 1900-2000 m, 20 Jun. 2007, *N. Gutiérrez 538* (NY); **Miranda**. Between Las Canales and El Eucanto, Nov. 1942, *T. Lasser 665* (G); Laderas y quebradas con restos de selva transicional al SE de Urb. Vista Linda, al E de Urb. Alto Hatillo, en las cabeceras del Río Guarita, 10°26'N, 66°49'W, 10 Aug. 1975, *J.A. Steyermark & P. Berry 111910-A* (NY); Los Salias, Carretera Panamericana, km 11, Altos de Pipe, 10°23'55"N, 66°58'27"W, 1565 m, 9 Nov. 2014, *R. Gonto & Á. Fernández 5902* (NY); **Monagas**. Cerro La Cueva, 1000 m, 29 Nov. 1987, *J. Bono 7230* (FT); **Táchira**. Entre Valle Paez y Betania, cerca la frontiera con Colombia, 15 Nov. 1975, *G.S. Bunting 4901* (NY); Sierra El Casadero, along Highway between Las Dantas and Las Adjuntas, 7°45'N, 72°25'W, 12 Nov. 1979, *J.A. Steyermark & al. 120079* (MO), *120152* (MO, NY); Parque Cazadero, Quebrada Cazadero, 16 km NW of San Cristóbal, 400-650 m, 7°54'N, 72°18'W, 2 May 1981, *R. Liesner & M. Guariglia 11694* (MO, VEN); Junín, Quebrada Agua Blanca, near La Rochela, along Delicias-Rubio Highway, 1850-2000 m, 72°26'W, 7°35'N, 15 Nov. 1982, *G. Davidse & A.C. Gonzalez 22347* (MO, NY); **Trujillo**. 34 km from Valera along road to Timotes, 14 Aug. 1964, *F.J. Breteler 4136* (US); Boconó, P.N. Guaramacal, vertiente nord a altura de 2100 m, bosque húmedo montano alto, Mar. 2003, *B. Stergios 19993* (K, US).

(11a) ***Lasiacis oaxacensis*** (Steud.) Hitchc. var. ***oaxacensis***, Proc. Biol. Soc. Wash. 24: 45. 1911. (Fig. 30).

Bas.: *Panicum oaxacense* Steud., Syn. Pl. Glum. 1: 73. 1854.

Type: *Mexico, Oaxaca, Lenormand s.n*. (holotype: P! [barcode P00633942]).

Description

Perennials, caespitose. *Culms* 0.5-2.0 m tall, creeping and rooting at the nodes, widely branched; *internodes* 2-5(-6) mm thick, partially hollow, glabrous, herbaceous; *nodes* glabrous. *Leaf sheaths* glabrous, one or both margins ciliate; *collars* usually puberulent or pubescent along the margins, hairs 0.5-2.0 mm long; *ligules* 2.0-6.0 mm long, prominent brown, appressed puberulent, sometimes hispid on the back, margins ciliate with hairs up to 2 mm long, apex ciliate and usually lacerate; *blades* 15-30 cm long, 1.5-2.5 cm wide, prominent, narrowly linear-lanceolate, acuminate, base asymmetrical, glabrous and scabrous along the midribs. *Panicles* 15-30 cm long, usually terminal; *branches* spreading, naked on the lower ½ or 2/3, bearing pedicellate spikelets usually in clusters at the end of the branchlets. *Spikelets* 3.6-4.5 mm long; *lower glumes* 1.5-2.4 mm long, 4-8-veined; *upper glumes* 2.5-3.5 mm long, 7-11-veined; *sterile florets* staminate, *lemmas* 8-10-veined, *paleas* ¾ to equal the fertile floret, *anthers* 1.0-2.3 mm long, *fertile florets* 3.5-3.8 mm long, 1.8-2.3 mm wide, *anthers* 1.6-2.3 mm long, white; *stigmas* purple; *caryopses* ca. 2.0 mm long, 1.5 mm wide. *Chromosome number*: $2n$ = 36 (Davidse 1972, 1978).

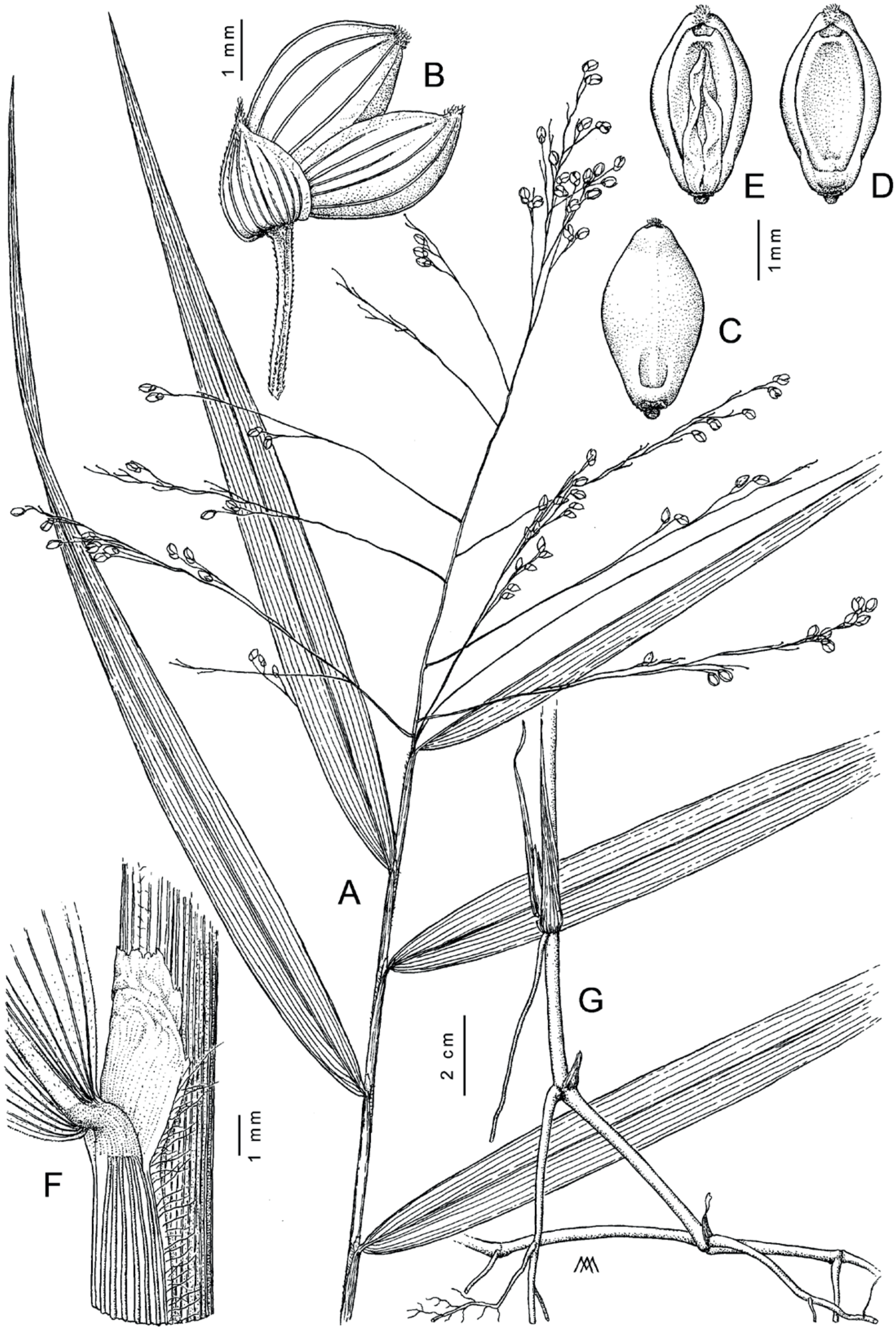

Figure 30. *Lasiacis oaxacensis* (Steud.) Hitchc. var. *oaxacensis*: **A.** Habit; **B.** Spikelet lateral view; **C.** Fertile upper floret dorsal view; **D.** Fertile upper floret ventral view without lower persistent palea; **E.** Fertile upper floret ventral view with lower persistent palea; **F.** Ligular area [A-F. from *T. Koyama & G.S. Bunting 14098* (NY)]; **G.** Culm rooting at the nodes [G. from *J.G. Hawkes & al. 2131* (G)]. *A. Maury delineavit.*

Vernacular names

Belize: Toledo, "*rat rice*" P.*H. Gentle 3937* (NY, US); **Ecuador**: Chimborazo, "*tundilla*" *M. Acosta Solís 5176* (US), Los Ríos, "*paja de saino*" *M. Acosta Solís 19481* (US); **Honduras**: Comayagua, "*zacate*" *A.I. Hernández 119* (MO); **Mexico**: Oaxaca, "*zacate de escobe*" *Souza 525* (Davidse 1978); **Perú**: San Martín, "*carricito castillo*" *J. Schunke Vigo 7001* (MO, US) .

Distribution

Belize, Colombia, Costa Rica, Dominican Republic, Ecuador, El Salvador, Guatemala, Haiti, Honduras, Jamaica, Mexico, Nicaragua, Panama, Perú, Venezuela. (Fig. 31).

Distribution (bibliographic references)

Hitchcock (1913); Hitchcock and Chase (1917); Hitchcock (1920, 1927a, 1930, 1936); Swallen (1931, 1936, 1943, 1955b); Standley (1937); Beetle (1977); Davidse (1978, 1994, 2001); Croat (1978); Pohl (1980); McVaugh (1983); D'Arcy (1987); Cialdella and Vega (1996); Serna and López-Ferrari (2000); Morales (2003); Zuloaga et al. (2003); Correa et al. (2004); Renvoize et al. (2006); Hokche et al. (2008); Giraldo-Cañas (2011); Acevedo-Rodríguez and Strong (2012); Villaseñor (2016); Dávila et al. (2018); Sánchez-Ken (2019); Menjivar et al. (2021).

Ecology

Forest edges and open areas inside the forest, roadsides and edges of plantations. From sea level to 1500 m.

Phenology

November through May. In southern America highlands mostly May through October/November.

Figure 31. *Lasiacis oaxacensis* (Steud.) Hitchc. var. *oaxacensis*: general geographic distribution.

Remarks

Lasiacis oaxacensis var. *oaxacensis* is closely related to *L. linearis* Swallen, but with a solid and procumbent culm, long and narrow leaves, robust midveins, and conspicuous ligules up to 6 mm long. Adventitious roots are more solid and developed than in *L. linearis*. The panicles are very large and with open, spreading branches. The distribution of *L. oaxacensis* var. *oaxacensis* goes from Mexico southward throughout Central America – including the Caribbean area (Jamaica and Haiti) - to South America in Colombia, Venezuela, Ecuador and Peru.

Selected Specimens

BELIZE. **Belize**. Tracie Rock, Sibun River, 21 Jan. 1936, *P.H. Gentle 1769* (K, NY); **Cayo**. Mt. Pine Ridge, 12 miles S of Georgeville, 600 m, 24 Jan. 1974, *R. Liesner & J. Dwyer 1588* (MO); **Stann Creek**. Near Hope Creek, 9 Feb. 1953, *P.H. Gentle 7874* (G, NY, US); In acahual, Tipparery Road, 12 miles Section, Stann Creek-Middlesex Road, 4 Feb. 1957, *P.H. Gentle 9331* (G); **Toledo**. Temash River, 4 Mar. 1935, *W.A. Schipp 1368* (BM, G, K, NY, US); Monkey River, 4 Mar. 1942, *P.H. Gentle 3937* (NY, US); On creekside, Crique Negro, Edwards Road beyond Columbia, 14 Feb. 1951, *P.H. Gentle 7205* (G, NY, US); Bladen Natire Reserve, NW BNR near the Bladen River, 45 m, 16°33'N, 83°43'W, 16 Feb. 1997, *S.W. Brewer 171* (MO).

COLOMBIA. **Chocó**. Novita, vereda Curundó, margen izquierda del Río Ingarà, 550 m, 1 Dec. 1983, *P. Franco & al. 1056* (MO); **Nariño**. Isla El Moro Grande, Pacific Coast near Tumaco, Jan. 1942, *E. Dryander 2555* (G); Santa Marta, ¿Nov.?, *H.H. Smith 2142* (BR, COL, G, K, L, MO, NY, US, W); **Risaralda**. Periera, Hacienda Alexandria, km 8 Cerritos-La Virginia, extremo norte de parte ancha del Valle del Río Cauca, 175 m, 04°51'N, 75°52'W, 6 Jan. 1995, *P. Silverstone-Sopkin & N. Paz 7401* (MO).

COSTA RICA. **Alajuela**. Carrillos de Poas cerca de Río Poas, 19 Nov. 1933, *A.M. Brenes 17380* (NY); In canyon, 1,5 km S of San Pedro de Poás, 1000 m, 3 Dec. 1968, *R.W. Pohl & G. Davidse 11522* (US); Between Cerro Chato and Cerro de Los Perdidos, 17 Feb. 1989, *G.F. Russell & al. 769* (MO); **Guanacaste**. El Arenal, 485-600 m, 18-19 Jan. 1926, *P.C. Standley & J. Valerio 45151* (US); **Heredia**. Finca La Selva, Río Puerto Viejo just E of its junction with the Río Sarapiqui, 7 Apr. 1980, *B. Hammel 8479* (MO); **Limón**. Guapiles, edge of rainforest, Aug. 1964, *H.S. McKnee 11101* (K, P, US); Canton de Talamanca, Cuenca del Sixaola, San Miguel, de la Estación Asacode, 100 m, 09°34'30"N, 82°40'00"W, 20 Jan. 1997, *J. Gonzalez 1688* (MO); Cuenca del Estrella, Reserva Biológica Hitoy Cerere, 100-200 m, 09°40'40"N, 83°01'25"W, 12 May 1999, *A. Rodríguez & al. 4896* (G, MO); **Puntarenas**. 12 km by road SE of Paso Real Ferry, E side of Río Terraba, 31 Dec. 1974, *R.W. Pohl 13121* (K); Monteverde, Cloud Forest Reserve, Cordillera de Tilaran, 1500-1620 m, 26 Sep. 1983, *W.Z. Pounds 74* (MO); Forests along S side of Quebrada Bonita, to ca. 1 km E of Costanera Highway, Carara Reserve, 30-40 m, 9°47'N, 84°37'W, 11 Jan. 1985, *M. Grayum 4736* (MO); Cantón de Osa, Los Mogos, 20 m, 8°45'00"N, 83°22'50"W, 12 Jan. 1991, *V. Ramírez 59* (MO, USJ); Cantón de Golfito, Jiménez, Río Piro, 50 m, 08°24'08"N, 83°20'25"W, 18 Jan. 1991, *E. Castro 168* (MO, USJ); Buenos Aires, Cuenca Terraba-Sierpe, Sendero a Cerro Cabecar, 2000 m, 9°19'15"N 83°23'21"W, 10 Sep. 2000, *E. Alfaro 3416* (MO); **San José**. Santa Maria de Bota, 4 Apr. 1890, *H. Pittier 2247* (G); San José, 22-24 Oct. 1911, *A.S. Hitchcock 8488, 8496* (US); Vicinity of El General, Jan. 1939, *A.F. Skutch 3821, 3863* (K, MO, NY, US).

ECUADOR. **Chimborazo**. Hacienda Rosa Mercedes, sobre Bucay, 500-850 m, 12 Aug. 1943, *M. Acosta Solís 5176* (US); **Esmeraldas**. Midway between Santo Domingo de los Colorados and Quinindé, 16 May 1955, *E. Asplund 16365* (G, K, NY, P, UPS, US); El Vichi, 11 Apr. 1981, *F.M. Valverde 6504* (MO); **Guayas**. Milagro, 50 m, 30 Jun.-2 Jul. 1923, *A.S. Hitchcock 20299* (NY, US); Panigon Plantation, 8 miles S of Milagro, 12 Jul. 1923, *A.S. Hitchcock 20568* (US); Vicinity of Guayaquil, Cerro Azul forest, 14 Jun. 1955, *E. Asplund 16632* (NY, UPS); Naranjal, Reserva Ecologica Manglares-Churute, Parroquia Taura, 100-350 m, 02°27'S, 79°40'W, 26 Sep. 1992, *C.E. Cerón & al. 20374* (MO); **Los Ríos**. Canton Vinces, 50 m, Oct. 1934, *Y. Mexia 6581* (BM, US); Pichilingue, 90 m, 12 Sep. 1950, *M. Acosta Solís 19481* (US); Between Babahoyo and Montale, secondary monsoon forest and cultivated land, 4-7. Aug. 1967, *B. Sparre 17983* (UPS); **Manabí**. s.d., *H.F.A. von Eggers 15572* (K, P); Vicinity of Ventura, 23-24 Oct. 1918, *J.N. Rose & G. Rose 23525* (NY, US); **Oro**. Between Santa Rosa and La Chorita, 0-100 m, 27 Aug. 1923, *A.S. Hitchcock 21131* (US); **Pichincha**. Along bank N of river 3 km W of Alluriquin, 800 m, 20 Oct. 1981, *L. Werling & S. Leth-Nissen 517* (MO, NY).

EL SALVADOR. **Ahuachapán**. San Benito, al E de las escaleras, 950 m, 13°49'N, 89°56'W, 8 Oct. 1993, *E. Sandoval 1467* (MO); San Benito, la Reforma, 23 Oct. 1994, *L.E. Escobar & E. Sandoval ISB00748* (K); **La Libertad**. Santa Tecla, 15 Jan. 1949, *L.O. Williams & A. Molina 15089* (US); Volcán de San Salvador, ca 2 km & below the crater, 1400 m, 6 Jun. 1970, *G. Davidse & R.W. Pohl 2026* (MO), **n = 18!** (Davidse 1978); Parque Nacional El Boquerón, El Boquerón, falda volcán de San Salvador, 13°44'03"N, 89°16'45"W, 1766-1831 m, 25 Jun. 2015, *J. Menjívar* & *R.M. Baldini 3404* (FT, MHES); **Morazán**. Montes de Cacaguatique, 2 Jan. 1942, *J.M. Tucker 694* (K); San Salvador, 20-26 Nov. 1911, *A.S. Hitchcock 8877* (NY, US); **San Miguel**. Volcán Cochagua, 1050 m, 13°16'N, 87°50'W, 31 Jan. 1998, *A. Monro & al. 2103 (*BM, MO); **Santa Ana**. 15-18 Nov. 1911, *A.S. Hitchcock 8853* (BM, US**); San Salvador**. San Salvador, 1922, *S. Calderón 507* (NY, US); Santo Tomás, 1922, *S. Calderón 1324* (MO, NY, US); Near bottom of crater of Volcán San Salvador, 8 Jan. 1951, *N.C. Fassett 28590* (US).

GUATEMALA. **Alta Verapaz**. Cubilquitz, Mar. 1904, *H. von Tuerckheim 8623* (K); **Guatemala**. Guatemala City, 1–3 Dec. 1911, *A.S. Hitchcock 9045, 9080, 9107* (NY, US); Guatemala City, 11 Nov. 1916, *F.W. Popenoe 735* (L, US); Guatemala, on dry hillside of River Villalobos, 12-23 Jan. 1966, *A. Molina & al. 16075* (NY, W); **Izabal**. Between Los Amates and Izabal, Sierra del Mico, 15 Feb. 1908, *W.A. Kellerman 7486* (NY, US); Vicinity of Quiriguà, 15-31 May 1922, *P.C. Standley 24122* (NY, US); North of Quiringuá, 2 Mar. 1932, *P. Weatherwax 1715* (BM); **Jutiapa**. Between Jutiapa and La Calera, SE of Jutiapa, 2 Nov. 1940, *P.C. Standley 76153* (K); **Petén**. Río Pasion, Altar de Sacrificios, 7 Feb. 1964, *C.L. Lundell 17788* (US); Petén, Sacate, fruto verde, en foresta alta, Dolores, en orillando el camino para caserio Sabaneta, a km 70, lado norte, 17 Feb. 1971, *R. Tún Ortíz 1598* (US); **Quetzaltenango**. In dumetis, Mazatenango, Nov. 1870, *G. Bernoulli 1189* (FI, G, NY); Mountains near Santa Maria, S of Quetzaltenango, 25 Mar. 1932, *P. Weatherwax 180* (K); **Sacatepéquez**. Near Las Lajas, 1200 m, 28 Nov. 1938, *P.C. Standley 58104* (US).

HAITI. **L'Artibonite**. Vicinity of Kalacroix, Section Dessalines, 700 m, 12 Dec. 1925, *E.C. Leonard 7997* (US); **Nord**. Massif du Nord, Morne Brigand, 10 Dec. 1924, *E.L. Ekman 2841* (US);

Vicinity of Marmelade, 800 m, 19 Aug. 1925, *E.C. Leonard 8192* (MO, US); Vicinity of Dondon, 6 Jan. 1926, *E.C. Leonard 8572* (NY, US); Vicinity of Plaisance, 400 m, 28 Jun. 1926, *E.C. Leonard 9391* (US); **Sud**. Massif de la Hatte, Marne Rochelois, Miragoane road, Buttel to Etang-Ray, 3 Nov. 1926, *E.L. Ekman 7153* (US); Morne Rochelois, 3 Nov. 1926, *E.L. Ekman H7153* (K).

HONDURAS. **Atlantida**. Common on Pajuiles riverbank, between Tela and Pajuiles, 11 Apr. 1970, *A. Molina & al. 25714* (NY, US); 7 miles E of Tela along road to La Ceiba, 28 Jun. 1970, *G. Davidse & R.W. Pohl 2205* (NY, US); **Comayagua**. Esquias, 75 km E de Comayagua, 550 m, 28 Dec. 1981, *A.I. Hernández 119* (MO); **Yoro**. 15 km SSE of Río Viejo along road to Olanchito, 27 Jun. 1970, *G. Davidse & R.W. Pohl 2199* (US); **Morazán**. Puente Colorado N of T. Large vine, 7 Dec. 1949, *P.C. Standley 24910* (NY); Montaña La Tigra, Presa La Tigra, 29 Nov. 1958, *J.G. Hawkes & al. 2131* (C, G); 12 km E of El Zamorano along Highway 4, 800 m, 18 Jun. 1970, *G. Davidse & R.W. Pohl 2127* (MO, US); **Olancho**. Poncaya, Pena Blanca Mountain, 4 Mar. 1982, *S. Blackmore & G.L.A. Heath 2014* (BM, MO). **Santa Barbara**. San Pedro Sula, Jul. 1888, *C. Thieme 5585* (US); Santa Barbara, 1 km de Santa Barbara, 11 Dec. 1950, *A. Molina 3676* (US); Between Zacapa and El Monchito, 30 Dec. 1978, *R.W. Pohl & M. Gabel 13827* (K, MO).

JAMAICA. **Clarendon**. Peckham, Upper Clarendon, 29 Dec. 1917, *W. Harris 12828* (K, MO, NY, US); **Portland**. Nanny Town site, 12 Dec. 1973, *C. Whitefoord 490* (BM, MO); **St. Ann**. Mt. Diablo, Feb. 1916, *H.N. Ridley 27* (MO); **St. Elizabeth**. Near Ipswich, 21 Oct. 1912, *A.S. Hitchcock 9608* (US); Hanover, Delphin Head, 21 Dec. 1960, *C.D. Adams 8632* (BM); **Trelawny**. Troy, 6 Nov. 1912, *A.S. Hitchcock 9800* (US); Teyre near Troy, 18 Oct 1917, *W. Harris 12615* (NY, US); **Westmorland**. Lindo's Hill, 18 Dec. 1914, *W. Harris 11832* (C, K, MO, NY, P, US).

MEXICO. **Chiapas**. Chiapas, Jilguero, Escuintla, 27 Nov. 1947, *E. Matuda 17286* (K, NY); Near the junction of the Río Perlas and Río Jataté at San Quintin and near Laguna Miramar, 22 Mar. 1955, *E.R. Sohns 1685* (K, US); Tuxtla Gutierrez, 17 km N of Tuxtla Gutierrez along road to El Sumidero, 27 Oct. 1965, *D.E. Breedlove 13903* (US); Ixtapa, near the Zinacantán, paraje of Muctajoc, 29 Oct. 1981, *D.E. Breedlove 54023* (NY); Angel Albino Corzo, slopes of Río Cuxtepec, below Finca Cuxtepec, 4 Nov. 1981, *D.E. Breedlove 54688* (NY); Mapastepec, Sierra de Soconusco, road to Tuxtla Gutierrez, 15°32'N, 92°48'W, 20 Jan. 1987, *T.B. Croat & D.P. Hannon 63325* (BM, MO, NY); San Fernando, 21 Oct. 1989, *J.C. Soto & al. 13327* (BM); Ocosingo, en Crucero de Lancanja-Tzeltal, camino Nuevo Guerrero a Santo Domingo, 340 m, 16°56'N, 91°14'W, 31 Jan. 2002, *E. Martínez S. 35169* (MO); **Colima**. Rancho El Jabali, 25 km NNW of Colima in the SW foothills of the Volcán de Colima, 1400 m, 19°26'N, 103°40'W, 9 Jan. 1991, *A.C. Sanders 10476* (MO); **Jalisco**. Wooded hills 2 miles above N of La Cuesta, road to Talpa de Allende, 19 Nov. 1960, *R. McVaugh 21157* (NY); Puerto Vallarta, 14 km al SE de P. Vallarta, 10 Nov. 1978, *J. Garcia & al. 929* (NY); **Michoacan**. Sierra Madre, 4 Nov. 1898, *E. Langlassé 556* (G, K, P, US); **Nayarit**. Mountains 9 miles N of Compostela, steep heavily forested stream valley in oak zone, 12 Nov. 1959, *R. McVaugh & W.N. Koelz 510* (G, NY, US); **Oaxaca**. Tuxtepec, Chiltepec and vicinity, Jul. 1940-Feb. 1941, *G. Martinez-Calderón 483* (US); Santa Maria Jacatepec, Tuxtepec, subida al Predio del Aquila, en San Augustin, 25 km al Ovest de la Reforma, carretera a Ayozintepec, 17°50'N, 096°06'W, 21 Feb. 1988, *R. Torres C. 11549* (US); **Veracruz.** Valleé de Cordoba, 1865-66, *E. Bourgeau 1461* (G, K, L, P), 1865-66, *E. Bourgeau 2648* (L); Vicinity of Zacuapan, Nov. 1906, *C.A. Purpus 2157* (MO, NY, US); Fortuño, Coatzacoalcos River, Mar. 1937, *L.O. Williams 8271* (G, P, US); Ca. 5 km S of Catamaco on Highway 180, 20 Feb. 1969, *M.L. Smith 1710* (VPI); Ixtaczoquiatlan, ca. 2 km E of town of Orizaba, S of old road between Fortìn and Orizaba, 18°51'N, 97°03'W, 7 Dec. 1983, *M. Nee 23843* (MO, NY); Hidalgotitlan, 1 km SE of Agustin Melgar, 17°15'N, 94°33'W, 2 Mar. 1984, *M. Nee 29773* (MO, NY); Las Choapas, 18 km E of Campamento La Laguna and 3 km ESE of bridge over Río Grande on main gravel road of Uxpanapa area, 17°16'N, 94°20'W, 4 Mar. 1984, *M. Nee & K. Taylor 29907* (MO, NY).

NICARAGUA. **Carazo**. Jinotepe, 3-7 Nov. 1911, *A.S. Hitchcock 8672, 8698* (NY, US); **Chinandega**. Volcán Chonco, 700-1100 m, 12°41'N, 87°02'W, 30 Oct. 1984, *P.P. Moreno 25020* (MO); Chinandega, Chichigalpa, Volcán Casita, sobre la loma El Coyol, 1320 m, 4 Feb. 2004, *I. Coronado & N. Gutierrez 454* (MO); **Chontales**. 2 km from Villa Sandino along road to Bulun, heavily disturbed evergreen forest, 310 m, 12°03'59"N, 84°58'51"W, 18 Jan. 2009, *W.D. Stevens & O.M. Montiel J. 27794* (MO); **Estelí**. Condega, Comunidad El Bramadero, Bosque Los Alpes, 400-500 m, 13°23'07"N, 86°15'42"W, 26 Jan. 2008, *J.G. Calderón Vindell 217* (MO); **Granada**. Volcán Mombacho, costado oeste, entre la hacienda El Progreso y las torres e comunicaciones, 700-1000 m, 7 Jan. 1983, *A. Grijalva & al. 2094* (MO); Granada, Reseva Natural Mombacho, Hacienda Cutirre, 400 m, 11°49'55"N 85°55'57"W, 23 Jan. 2004, *R. Rueda & D. Paguaga 17748* (M); **Jinotega**. Bocay, Reserva Natural Kilambé, San Miguel de Kilambé, 700-900 m, 13°31'N, 85°37'W, 6 Jan. 2001, *R. Rueda & al. 15225* (MO); Wiwili, Comunidad La Esperanza, Reserva Bosawas, Territorio Miskito Indian Tasbabay Kum, parcela 1, 1 kn al W de la finca de Leonidas Bodin, 60-70 m, 23 Feb. 2008, *J. Prado M. 223* (MO); **Managua**. Sierra de Managua, s.d., *Bro. A. Garnier 39* (US); **Matagalpa**. Macizos de Penas Blancas, SE side, drainage of Quebrada El Quebradon, slopes N and W of Hacienda San Sebastian, 800-1100 m, 13°14'N, 85°38'W, 20-21 Jan. 1982, *W.D. Stevens & al. 21238* (MO); **Rivas**. Isla Omotepe, Volcán Maderas, subiendo por la hacienda de Merida, 600-1000 m, 11°26'N, 83°31'W, 16 Jan. 1985, *W. Robleto 1711* (MO); **Río San Juan**. El Castillo, Río Romeron, 1 km al W de la comunidad Las Maravillas, 100 m, 11°07'15"N, 84°21'04"W, 25 Jan. 2005, *R. Guzmán 765* (MO); **Zelaya**. Vicinity of La Luz-Siuna, 11 Mar. 1961, *G.S. Bunting & L. Licht 527* (NY); Zelaya, Intersection of road to Puerto Cabezas-Waspan & Río Lecus, 100 m, 14 Jul. 1970, *G. Davidse & R.W. Pohl 2346* (MO); Zelaya, Suna, Caño El León, Carretera al Hormiguero, 2 Feb. 1983, *F. Ortiz 738* (MO).

PANAMA. **Bocas del Toro**. 8 Feb. 1911, *M.A. Carleton 166* (NY); Almirante, 1928, *G. Proctor 105* (NY, US); Old Bank Island, 14 Feb. 1941, *H. von Wedel 2086* (MO, US); Islas San Cristobal, Cerro de Bocatorito, 11 Feb. 1989, *P.M. Peterson & C.R. Annable 6767* (US); Approximately 3.5 km S of Tiger Key on the mainalnd, 100 m, 23 Feb. 1989, *P.M. Peterson & C.R. Annable 7032* (MO); 5 km S of Tiger Key on the mainland near Cacao Boquete just N of Ensenada de Boquete, 5-110 m, 24 Feb. 1989, *P.M. Peterson & C.R. Annable 7071* (MO); 2 km W of Bocatorito, 5-80 m, 3 Mar. 1989, *P.M. Peterson & C.R. Annable 7312* (MO); **Chiriquí**. Chiriquí Volcán, 29-30 Sep. 1911, *A.S. Hitchcock 8199, 8201* (NY); Edge of open pasture and thicket of trees along creek, Monte Verde, 2.5 km W of Puerto Armuelles, 80 m, 18 Feb. 1973, *R.L. Liesner 64* (MO); Large meadow adjacent to Río Caldera just N of Boquete, 1060 m, 9 Mar. 1989, *P.M. Peterson & C.R. Annable 7377* (US); Boquete, road Boquete-Bajo Mono-Alto Chiquero, entrance to Sendero Los Quetzales, Alto Chiquero, by the roadside, cloud forest, 08°50'34"N, 82°28'56"W, 2532 m, 20 Jan. 2011, *A. Freire-Fierro 3613* (PMA); Carretera de Alto Boquete-El Salto, 8°46'30"N, 82°27'28"W, 1437 m, 24 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 904* (FT, SCZ); **Colón**. Between France Field and Catival, 9 Jan. 1924, *P.C. Standley 30230* (US); 4 km ENE of Buena Vista, along road to Sardinilla, 100 m, 30 Dec. 1973, *M. Nee 9124* (MO); **Darién**. Clearing at confluence of Río Chucanaque and Río Canclones, 5 Jul. 1962, *J.A. Duke 5107A* (MO); **Herrera**. Middle area of Río Guanaco, 8 Feb. 1966, *J.S. McCorkle C-126* (US); **Panamá**. Canal Zone, Hilly Foresta round the Agua Clara Reservoir, near Gatún, 5 Feb. 1911, *W.R. Maxon 4653* (L, NY, US); Canal Zone, forest above Sabana de El Salto, on the trail to Camp Aguacatal, eastern slope of Chiriquí Volcán, 10-13 Mar. 1911, *W.R. Maxon 5266* (NY); Canal Zone, Gatún Lake, 15 Dec. 1911, *A.S. Hitchcock 412* (BM, F, G, K, L, P, MO, NY, US, W); Canal Zone, vicinity of Frijoles, *E.P. Killip 4284* (US); Canal Zone, along the Río Chilibre, 26 Feb. 1923, *C.V. Piper 5288* (US); Canal Zone, Cerro Gordo, near Culebra, 5 Dec. 1923, *P.C. Standley 26009* (MO, US); Canal Zone, Gamboa, 26 Dec. 1923, *P.C. Standley 28535* (US); Canal Zone, Darién Station, 19 Jan. 1924, *P.C. Standley 31609* (US); Canal Zone, Banks of Chagres, 18 Dec. 1924, *F.W. Popenoe 32* (NY); Canal Zone, Armour Trail, 10 Jan. 1940, *F.W. Hunnewell 16395* (NY); San José Island, Pearl Archipelago, 18 Jun. 1945, *C.O. Erlanson 308* (G, NY, US); San José Island, Perlas Arch., 55 mi. SSE of Balboa, 26 Dec. 1945, *I.M. Johnston 904* (BM, US); Canal Zone, Fort Clayton, vicinity W end Gatun Lake dam, 22 Dec. 1965, *J. Dwyer 1967* (MO); Canal Zone, Albrook forest, TTC tower site, 20 Jun. 1966, *K.E. Blum & J.D. Dwyer 2089* (MO, SCZ); Perlas Islands, Sunny river bank, Playa Grande, San Jose Island, 18 Dec. 1968, *E.L. Tyson & H. Loftin 5061, 5070* (MO, SCZ); Canal Zone, Barro Colorado Island, 10 Jan. 1969, *T.B. Croat 7081* (MO, SCZ); Panamá, near TV tower on Continental Divide on ridge of Cerro Penon, 3 km S of Alcade Diaz, 440 m, 18 Dec. 1973, *M. Nee 8853* (MO, PMA); Panamá, base of Serrania de Cañazas, ca. 15 km SW of Cañaza near Río Torti, 150 m, 8°52'N, 78°22'W, 15 Jan. 1983, *B.A. Stein 1376* (MO); Canal Zone, secondary forest across from Curundu High School, 9°02'N, 79°31'W, 19 Jan. 1990, *T.B. Croat 69848* (MO, PMA); Panamá, Parque Nacional Soberanía, camino del Oleoducto, 9°07'11"N, 79°42'52"W, 78 m, 27 Jan 2012, *M.N.S. Stapf & R.M. Baldini 915* (FT, PMA).

PERÚ. **Huanuco**. Tingo Maria, 12 Aug. 1940, *E. Asplund 12197* (G, K, UPS, US); **Junín**. Along Río Perene, near "Hacienda 3", Colonia Perene, 16-18 Jun. 1929, *E.P. Killip & A.C. Smith 25170* (NY, US); **San Martín**. Mariscal Cáceres, Quebrada de Huaquisha (margen Izauierda del Río Huallaga), 400 m, 25 Jun. 1974, *J. Schunke Vigo 7001* (K, L, MO, US); Mariscal Cáceres, Tocache Nuevo, Fondo Miramar along Río Huallaga, 450 m, 3 Jul. 1978, *T.C. Plowman & J. Schunke Vigo 7558* (K, US); Lamas, Alonso de Alvarado, Comino a Roque, 3-4 km de San Juan de Pacaizapa, 3 Jul. 1977, *J. Schunke Vigo 9758* (K, MO).

VENEZUELA. **Aragua**. Guamitas, 29 Dec. 1938, *A.H.G. Alston 5766* (BM); Aragua, Guamitas, Parque Nacional, 780 m, 21 Jan. 1946, *H. Pittier 15209* (US); Aragua, Parque Nacional Rancho Grande, on Rd. 3 to Pto. Cabello, ca. 16 miles from Maracay, 4 Dec. 1969, *T. Koyama & G.S. Bunting 14098* (MO, NY, US); Aragua, 8 km NW of Rancho Grande along road to Cata, cloud forest, 720 m, 15 Nov. 1971, *G. Davidse 3113* (MO); Aragua, Parque Nacional Henri Pittier, Rancho Grande, 1150 m, 12 Dec. 1973, *G. Davidse & M. Ramia 4980* (MO, US); **Barinas**. **Carabobo**. Chemnin de Valencia, Dec. 1843, *N. Funck 813* (G); Bejuma, Cordillera de la Costa, N de Bejuma, Carretera via Palmichal, 10°17'N, 68°15'W, 720-750 m, 27 Dec. 2010, *W. Meier & N. Flauger 16899* (G, US); **Guárico**. Roscio, Monumento Natural Cerro Platillón (Juan Germán Roscio), W de San Juan de Los Morros, 9°51'N, 67°30'W, 14 Dec. 1999, *W. Meier & D. Elsner 6212* (G); **Mérida**. Tycoporo forest reserve, 70°35'W, 8°15'N, 11 Dec. 1963, *F.J. Breteler 3* (G, NY, P, UPS); **Miranda**. Parque Nacional Guatopo, 13 Feb. 1973, *T.B. Croat 21700* (MO); Cerros del Bachiller, near E end, semi-deciduous forest between Quebradas Corozal and Santa Cruz, S of Santa Cruz, 8-20 m, 10°09'N, 65°48'W, 18-19 Mar. 1978, *J.A. Steyermark & G. Davidse 116381* (MO); **Yaracuy**. Bruzual, Montaña de Maria Lionza, 250-260 m, 10°07'N, 68°55'W, 12 Mar. 1981, *J.A. Steyermark & al. 124922* (MO); **Zulia**. Entre Las Tres Marias, y el Río Chiquito, 10°25'N, 70°55'W, 14-16 Feb. 1980, *G.S. Bunting 8990* (MO, NY).

(11b) *Lasiacis oaxacensis* (Steud.) Hitchc. var. ***maxonii*** (Swallen) Davidse, Ann. Missouri Bot. Gard. 64: 375. 1977.

Bas.: *Lasiacis maxonii* Swallen, Ann. Missouri Bot. Gard. 30: 231. 1943.

Type: "*Panamá, Chiriquí, vicinity of El Boquete, in thickets along wet trail, 1000-1300 m, 2-8 Mar. 1911, W.R. Maxon 4999*" (holotype: US! [barcode US00134115]; isotype MO! [Acc. No. MO128806]).

Description

Perennials, caespitose. *Culms* 0.5-2.0 m tall, creeping and rooting at the nodes, widely branched; *internodes* 2-5(-6) mm thick, partially hollow, glabrous, herbaceous; *nodes* glabrous. *Leaf sheaths* glabrous; *collars* glabrous or puberulent; *ligules* 0.5-1.0(-2.0) mm long, apex ciliolate, or ciliate with small hairs 1.0 mm long, margins ciliate; *blades* 15-25 cm long, 1.0-2.6 cm wide, acuminate, glabrous or scabrous on both surfaces, margins scabrous. *Panicles* 20-35 cm long, open, loosely flowered. *Spikelets* 3.5-4.0 mm long, distally paired in the branchlets, spreading, often purple; *lower glumes* 1.6-2.4 mm long, 4-8-veined; *upper glumes* 2.4-3.4 mm long, 7-11-veined; *sterile florets* staminate, *lemmas* 7-8-veined, *paleas* ¾ to equal the fertile floret, *anthers* 1.0-2.3 mm long; *fertile florets* 3.5-3.8 mm long, 1.8-2.3 mm wide, *anthers* 1.6-2.3 mm long, whitish, *stigmas* purple; *caryopses* ca. 2.0 mm long, 1.5 mm wide. *Chromosome number*: $2n = 36$ (Davidse 1972, 1978).

Distribution

Costa Rica, Honduras, Mexico, Nicaragua, Panama.

Distribution (bibliographic references)

Swallen (1943); Davidse (1977, 1978, 1994, 2001); Pohl (1980); D'Arcy (1987); Morales (2003); Zuloaga et al. (2003); Correa et al. (2004); Dávila et al. (2018); Sánchez-Ken (2019).

Ecology

Forests edges, a pioneer species in open areas inside cloud forests. Elevation between 500-1400 m.

Phenology

October through January, occasionally June (Honduras).

Remarks

Lasiacis oaxacensis var. *maxonii* differs from var. *oaxacensis* in having shorter ligules up to 1.0 mm long (rarely to 2.0 mm long), scandent culms, and loosely flowered panicles. I agree with Davidse (1978) to consider *L. maxoni* Swallen at infraspecific rank of *L. oaxacensis*. The distribution of var. *maxonii* (Swallen) Hitchc. is limited to Central America including Honduras, Nicaragua, Costa Rica, Panama, within the range of *L. oaxacensis*. In Panama this taxon is very frequent in Chiriquí, at the border with Costa Rica.

Selected specimens

COSTA RICA. **Alajuela**. In canyon, 1.5 km S of San Pedro de Poas, 1000 m, 3 Dec. 1968, *R.W. Pohl & G. Davidse 11522* (MO); **Cartago**. Tucurrique, à Las Vueltas, Dec. 1890, *A. Tonduz 12858 bis* (G, NY); **Guanacaste**. Vicinity of Tilaran, 10-31 Jan. 1926, *P.C. Standley & J. Valerio 44523* (US); **Puntarenas**. Quebrada Seca, Cerro Zapotal Miramar, 18 Sep. 1985, *L.G. Gomez & al. 24501* (MO); Canton de Puntarenas, Monteverde, pacific slope, moist forest, 1350 m, 10°18'N, 84°48'W, 17 Dec. 1989, *W.A. Haber 9616* (MO); **San José**. Río Torres à San Francisco de Guadalupe, Dec. 1895, *A. Tonduz 7199* (US); San Pedro, 25 Jan. 1922, *J.M. Greenman & M.T. Greenman 5289* (US); San José, vicinity of El General, Dec. 1935, *A.F. Skutch 2226* (K, MO, US); Along the Río Birillo about 1 km S of Santa Domingo, 21 Dec. 1974, *J. Taylor 17404* (NY).

HONDURAS. **El Paraiso**. Montaña Agua Fria, 14 Mar. 1963, *A. Molina 11338* (US); **Yoro**. 15 km SSE of Río Viejo along road to Olanchito, 27 Jun. 1970, *G. Davidse & R.W. Pohl 2199* (MO, NY), **n = 18!** (Davidse 1978).

MEXICO. **Jalisco**. Guadalajara, 30 Oct. 1888, *C.G. Pringle 1732* (G, K, UPS); **Morelos**. Salto de San Anton prope Cuernavaca, 9 Jan. 1926, *G.J.N. Woronow 2460* (US); **Tabasco**. Huimanguillo, SO of Malpasito, 1 Feb. 2002, *Calónico & al. 21308* (BM); Tabasco, Teapa, 1 km NE of Puyacatengo, 4 Feb. 2002, *Martínez 34872* (BM).

NICARAGUA. **Carazo**. Jinotepe, 5-7 Nov. 1911, *A.S. Hitchcock 8695* (BM, US); **Jinotega**. Macizos de Penas Blancas, vicinity of Finca of Manuel Estrada (El Cielo), 1200-1400 m, 13°15'N, 85°41'W, 13-18 Jan. 1979, *W.D. Stevens & al. 11474* (MO); **Matagalpa**. Sta. Maria de Ostuma, Cordillera Central de Nicaragua between Matagalpa and Jinotega, Dept. Matagalpa, 19-21 Feb. 1963, *L.O. Williams & al. 24776* (G); 7 km al SE de la ciudad, 1100 m, 12°52'N, 85°53'W, 9 Jan. 1981, *M. Guzmán & D. Castro 1614* (MO); **Rivas**. Isla Omotepe, Volcán Concepcion, lava del volcán en el sector de Santa Rosa, 700-900 m, 11°32'N, 85°36'W, 30 Oct. 1984, *W. Robleto 1494* (MO).

PANAMA. **Chiriquí**. Vicinity of El Boquete, 1000-1300 m, Sep. 28-Oct. 7 1911, *A.S. Hitchcock 8281* (US); Between Hato del Jobo and Cerro Vaca, 700-1000 m, 25-28 Dec. 1911, *H. Pittier 5422* (US); Planos de Hornitos, orillas de la carretera Gualaca-Fortuna, 8°38'13"N, 82°12'41"W, 1024 m, 20 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 854, 856* (FT, SCZ); Volcán, carretera Aguacatal, SW del Volcán Barú, 8°47'36"N, 82°34'54"W, 2079 m, 23 Jan 2012, *M.N.S. Stapf & R.M. Baldini* 878 (FT, SCZ); Carretera Volcán-Río Sereno, puente sobre el Río Chiriquí Viejo, 8°48'27"N, 82°40'W, 1338 m, 23 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 898* (FT, SCZ); Carretera Boquete-Alto Quiel, 8°48'03"N, 82°27'26"W, 1313 m, 24 Jan 2012, *M.N.S. Stapf & R.M. Baldini 899* (FT, SCZ); **Coclé**. El Valle de Antón, 1000-2000 ft, 2-3 Dec. 1967, *W.H. Lewis & al. 2594* (MO); Coclé, village of El Valle, 4 Jan. 1974, *J.D. Dwyer & M. Nee 11942 A* (MO, NY); **Panamá**. Camino Chiva-Chiva, entre Ave. Gaillard y Ave. Centenario, 9°01'15"N, 79°35'44"W, 62 m, 27 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 911, 913* (FT, SCZ).

(12) *Lasiacis pohlii* (Davidse) Baldini**, stat. nov.** (Fig. 32, 33).

Bas.: *Lasiacis rugelii* (Griseb.) Hitchc. var. *pohlii* Davidse, Ann. Missouri Bot. Gard. 64: 375. 1977. -

Type: "*Costa Rica, Cartago, 1 km NE of Pejibaye, along Río Pejibaye, growing at base of tree, ca. 700 m, 2 Nov. 1968, Pohl & Davidse 11478*" (holotype: ISC (photo!); isotypes CR (n.v.) [Acc. No. 50468], EAP (n.v.), MO! [barcode MO128803]).

Description

Perennials, caespitose. *Culms* 1-5 m long, glabrous, not conspicuously zigzagging (as in *L. rugelii*), erect at the base, arching and climbing upward into vegetation; *internodes* 3-6(-7.0) mm thick, hollow, glabrous or with a tight line of hairs on one side; *nodes* glabrous. *Leaf sheaths* pubescent, overlapping margin with hairs 1.0 mm long, auricular hairs 1.5-1-8 mm long; *collars* hairy at the base, hairs up to 1.0-1.3 mm long, collars forming a pseudopetiole 1.4 mm long; *ligules* inconspicuous, 0.2-05 mm long, membranous, glabrous; *blades* 4-8 cm long, 0.7-1.5 cm wide, ovate-lanceolate, acuminate, base asymmetrical, narrowed to truncate, adaxial surface glabrous, abaxial surface glabrous or minutely puberulent, margins scabrid. *Panicles* 3-8 cm long, usually not completely exserted; *branches* ascending to spreading; *pedicels* usually scabrid. *Spikelets* 3.5-4.4 mm long, globose, deep purple at maturity; *lower glumes* 1.7-2.5 mm long, 7-9-veined; *upper glumes* 2.3-3.3 mm long, 9-veined; *sterile florets* without flowers, *lemmas* 9-veined, *paleas* ½ to 2/3 the length of the fertile floret, pilose at the apex; *fertile florets* 3.8-4.5(-4.8) mm long, 2.4-2.8 mm wide, brownish, *anthers* 2 mm long, whitish, *stigmas* white; *caryopses* 2.2-2.5 mm long, 2.0-2.2 mm wide. *Chromosome number*: unknown.

Figure 32. *Lasiacis pohlii* (Davidse) Baldini: **A1.** Habit with fertile branches; **A2.** Lateral terminal branch [A1-A2. from *T.R. Soderstrom 2012* (K)]; **B**. Spikelet lateral view; **C**. Fertile upper floret dorsal view; **D**. Fertile upper floret ventral view without lower persistent palea; **E**. Fertile upper floret ventral view with lower persistent palea; **F**. Ligular area [B-F. from *T.B. Croat 25353* (K)]. *A. Maury delineavit*.

Figure 33. *Lasiacis pohlii* (Davidse) Baldini: habit and mature black spikelets. (Panama, Cerro Jefe, photo R.M. Baldini).

Iconographs

Fig. 108 as *L. rugelii* (Griseb.) Hitchc. var. *pohlii* Davidse (Pohl 1980).

Distribution

Costa Rica, Guatemala, Honduras, Mexico, Nicaragua, Panama. (Fig. 34).

Distribution (bibliographic references)

Davidse (1977, 1978, 1994, 2001); Pohl (1980); D'Arcy (1987); Serna and López-Ferrari (2000); Zuloaga et al. (2003); Correa et al. (2004); Dávila et al. (2018); Sánchez-Ken (2019). All references as *L. rugelii* (Griseb.) Hitchc. var. *pohli* Davidse.

Ecology

Edges of cloud forests, sometimes edges of open cultivated areas (Panama). Sea level up to ca. 900 m [Panama: *M.D. Correa & al. 7365* (MO, SCZ)].

Figure 34. *Lasiacis pohlii* (Davidse) Baldini: general geographic distribution.

Phenology

April through January.

Remarks

Lasiacis pohlii is related to *L. rugelii* and easily recognizable and distinct from the latter in having glabrous or short puberulent culms not conspicuously zigzagging, smaller panicles, and globose spikelets. Originally described as a variety (Davidse 1977), it is here elevated to the rank of species. *L. pohlii* is more widespread in Central America than in Mexico, with most finds in Costa Rica and Panama whereas *L. rugelii* is more common in northern Central America and the Caribbean (see also Davidse 1978). No isotype (R. J. Soreng *pers. comm.*) was found at US contrary to what stated in Davidse (1978).

Selected Specimens

COSTA RICA. **Alajuela**. Canton de San Carlos, Cordillera de Tilaran, 3-4 km W of La Tigra, 400-600 m, 10°21'00"N, 84°37'00"W, 18 Nov. 1993, *W. Haber 11702* (MO); **Cartago**. Bassin du Reventazon, bords du Rio Tuís, Sep. 1893, *A. Tonduz 8186* (G); Buíssons et broussailles de Tuìs, Nov. 1897, *A. Tonduz 11397* (G); Vicinity of Pejivalle, 600-850 m, Jan. 1940, *A.F. Skutch 4655* (MO, US); Canyon of Río Reventazón near Turrialba, 6 Aug. 1968, *R.W. Pohl & G. Davidse 10829* (K, US); Turrialba, 20 Oct. 1974, *M. Montiel 20 (pro parte)* (USJ); Valle du Reventazon, 19 Nov. 1890, *Biolley 3114* (G); **Guanacaste**. Canton de La Cruz, P.N. de Guanacaste, Estación Pitilla, 700 m, 11°02'N, 85°24'30"W, 7 Oct. 1990, *P. Rios 80* (MO); **San José**. Vicinity of El General, Jan. 1939, *A.F. Skutch 3862, 4040* (K, MO, NY, US).

GUATEMALA. **Alta Verapaz**. Cubilquitz, Aug. 1903, *H. von Tuerckheim 8620* (K, NY); Alta Verapaz, Cubilquitz, Oct. 1906, *H. von Tuerckheim 1481* (BM, FI, G, L, MO, P, US); **Izabal**. Bois de Las Pavas, valleè du Raventazon, Nov. 1890, *H. Pittier 3114* (US); Vicinity of Quiriguá, 15-31 May 1922, *P.C. Standley 23712* (US); **Guatemala**. Baja Verapaz, Purulha, along Highway CA14 between El Progresso and Coban, 3 miles S of Purulha, 17 miles N of junction with Highway 17 to Salamá and San Jeronimo, vicinity km/marker 160, 1620-1720 m, 15°13'N, 90°12'W, 26 Jan. 1987, *T.B. Croat & D.P. Hannon 63734* (MO).

HONDURAS. **Comayagua**. Quebrada el Agua Helada, 25 km NE de Comayagua, 13 Apr. 1985, *H.J. Ramos 187* (NY); Comayagua, La Misión, 10 km NW of Siguatepeque, 22 Oct. 1988, *Montoya 42* (BM); **Morazán**. Alrededores Col. Kennedy, 30 Jan. 1985, *V.M. Figueroa 164 (*NY).

MEXICO. **Chiapas**. Ocosingo, 5 km SW of Santo Domingo, 13 May 1982, *G. Davidse & al. 20402* (BM, MO); Chiapas, Tuxtla, Gutiérrez Mirador, 20 Oct. 1989, *A. Reyes Garcías & al. 1278* (BM); **Tabasco**. Teapa, NE of Cocona, 2 Feb. 2002, *Martínez 34852* (BM).

NICARAGUA. **Jinotega**. Wiwili, Comunidad Boca de Plis, Reserva Bosawas, Territorio Indian Tasbaika Kun, parcela 1, finca de Natividad Urbina, 500 m al sur de la comunidad, 200-300 m, 4 Nov. 2007, *G.M. Martinez 45* (MO); Wiwili, Reserva de la Biosfera de Bosawas, Comunidad de Inipuwas, alrededor del transecto Yalu, 250 m, 14°24'N, 85°08'W, 24 Nov. 2008, *I. Coronado & al. 4974* (MO); **Zelaya**. Bosque lluvioso de montañas de Esquipulas y Aleman, drenaje de Río Aleman, 27-29 Nov. 1951, *P.J. Shank & A. Molina 4755* (US).

PANAMA. **Bocas del Toro**. Almirante, just N of Dos Milla, hillside, high climbing vine, 20 Aug. 1967, *S. McDaniel 5121* (MO); **Coclé**. La Mesa, 5 miles N El Valle, 10 Nov. 1965, *E.L. Tyson & al. 2422* (NY, SCZ); El Valle de Antón at the foot of Cerro Pilón, ca. 2000 ft, 15 Aug. 1967, *J.D. Dwyer & A. Correa 7974* (K, MO, US), *7978* (MO, US); La Mesa above El Valle de Antón, 1000 m, 14 Sep. 1968, *R.E. Weaver & R.B. Foster 1657* (MO, US); Hills above El Valle de Antón, 13 Aug. 1972, *W.G. D'Arcy & J.J. D'Arcy 6748* (C, MO, PMA); El Valle, 800 m, 17 Jan. 1973, *T.R. Soderstrom 2012* (K, MO, US); Coclé, tropical wet forest, La Mesa, 4 km N of El Valle, 875 m, 12 Feb. 1974, *M. Nee & M. Hale 9616* (MO); La Messa above El Valle, in forest on both sides of junction with road to Cerro Pilón,, 800 m, 21 Jul. 1974, *T.B. Croat 25353* (K, MO, US); La Mesa, above El Valle de Antón, ca. 2 km W of Cerro Pilón on slopes of steep hill, 860-900 m, 21 Jul. 1976, *T.B. Croat 37418* (MO); 700 m, 7,2 km from El Valle, main road along the Mesa Road, 18 Dec. 1977, *J.P. Folsom & al. 6932* (MO, US); La Mesa road N of El Valle, along stream gorge, 2700 ft, low cloud forest, 6 May 1981, *K. Systma & al. 4358* (F, MO); El Valle de Antón, La Mesa, faldas de Cerro Pilón, 8°38'29"N, 80°06'48"W, 825 m, 16 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 820* (FT, SCZ); **Panamá**. 2-3 miles S of Goofy Lake, road to Cerro Jefe, 2000-2200 ft, 10 Dec. 1966, *W.H. Lewis & al. 244* (K, MO, US); Cerro Campana, vicinity of Fla. State building, 10 Sep. 1970, *T.B. Croat 12142* (MO, NY, SCZ); Cerro Campana at end of road beyond Su Lin Hotel, 9 Apr. 1971, *T.B. Croat 14221* (MO); Cerro Azul, in forest, 23 Jun. 1972, *T.B. Croat 17287* (MO); Cerro Jefe, 700 m, 17 Nov. 1975, *G. Davidse & W.G. D'Arcy 10103* (K, MO, US); In ridge top forest remant 10 km N of Margarita (near Chepo) on road to Madrono, 1400 ft, 14 Oct. 1978, *B. Hammel & W.G. D'Arcy 5125* (MO); Cerro Jefe, 1.5 miles down right turnoff 6.7 miles past Goofy Lake, disturbed cloud forest, 700 m, 27 Dec. 1980, *K. Systma & W. Hahn 2901* (BM, K, MO, NY); Cerro Campana, 2500 ft, 17 Aug. 1982, *W.G. D'Arcy & C. Hamilton 14961* (MO); Cerro Campana, 700 m, 8°40'N, 79°55'W, 8 Sep. 1982, *C. Hamilton & al. 1189* (MO); Parque Nacional Cerro Campana, 2 km N of Highway 707, cloud forest, 850 m, 842'N, 7955'W, 1 Jan. 1983, *B.A Stein & C.W. Hamilton 1134* (MO); W of Inter-American Highway near Capira, Cerro Campana, ca. 900 m, 8°40'N, 79°50'W, 11 Nov. 1985, *G. MacPherson 7459* (MO, PMA); Parque Nacional La Campana, Cerro Campana, Sender de Interpretation, 1 km al E del Campamento de los guardabosques de INRENARE, 8°40'N, 79°55'W, 800-900 m, 30 Aug. 1990, *M. Correa & al. 7365* (MO, SCZ); Parque Nacional La Campana, Cerro Campana in the Mirador on La Cruz trail, tropical rain forest, 780 m, 8 Apr. 2002, *J.G. Sánchez-Ken 678* (BR, PMA, MO, US); Cerro Jefe en el camino a las cabañas 4 x 4, 9°13'30"N, 79°21'42"W, 767 m, 13 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 799* (FT, PMA, SCZ); Panamá Parque nacional Altos de Campana, alrededores de la intersection del sendero Cerro de la Cruz con el Sendero Panamá, 8°41'13"N, 79°55'16"W, 960 m, 14 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 810* (FT, PMA, SCZ); Cerro Jefe a Altos de Pacora, 9°13'51"N, 79°21'28"W, 742 m, 12 May 2012, *M.N.S. Stapf & al. 921* (FT, SCZ).

(13) *Lasiacis procerrima* (Hack.) Hitchc., Proc. Biol. Soc. Wash. 24: 145. 1911. (Fig. 35).

Bas.: *Panicum procerrimum* Hack., Oesterr. Bot. Z. 51: 431. 1901.

Type: "*Costa Rica, inter frutices ad fluvium Tilirì rope La Verbena et Alajuelita, 1000 m, Aug. 1894, Pittier 8819*" (holotype: W! [Acc. No. W19160024376]; isotypes: BR [(photo!) barcode BR000000686254], G! [barcode G00614228], US! Fragment from W [barcode US00139895], US! Three sheets [barcode US00147980, US00956499, US00956500 as collection number "*A. Tonduz 8819*"]).

Nomina nuda

Panicum scariosum Trin. ex Steud., Nomencl. Bot., ed. 2, 2: 263. 1841, *nom. nud*.

The specimen at G! [barcode 00614207]: "*Mexico, Hacienda de la Laguna*" in sched. "*Panicum scariosum* Trin. in Litt., an varietas *P. latifolium*? *Leg. Schiede et Depper, Communicavit Schhetendal* ["Schlechtendal"] *1842*", confirms the correct correspondence of *P. scariosum* to *L. procerrima* (Hack.) Hitchc.

Description

Perennials, often short-lived, caespitose. *Culms* 1.0-6.0(-6.5) m long, unbranched, with prop adventitious roots at the base or in clumps, decumbent, rooting at the nodes below; *nodes* 5-12(-14) mm thick, hollow, glabrous, or often puberulent lower at the nodes, herbaceous to lignified. *Leaf sheaths* glabrous or slightly puberulent, sometimes hispid, overlapping sheath margins ciliate at the apex with hairs 0.8-2.3 mm long, rarely glabrous, sheath auricles up to 2.3 mm long, pubescent to ciliate; *collars* glabrous to slightly pubescent; *ligules* 0.5-2.0 mm long, glabrous and slightly ciliate; *blades* 15-40(-45) cm long, 1.5-4.5(-5.0) cm wide, linear-lanceolate glabrous, slightly hispid, often abaxially velutinous and glaucous, acuminate, base cordate, clasping the stem, glabrous, often ciliate with hairs up to 2.5 mm long, margins scabrid. *Panicles* 20-120(-130) cm long, conspicuous, peduncles exserted; *branches* diffuse, glabrous, scabrous, bearing few spaced sessile or short-pedicelled spikelets; *pedicels* slightly scabrid. *Spikelets* 3.0-4.0(-5.0) mm long, 1.5-2.8 mm wide, ovate, suberect; *lower glumes* 1.5-2.4 mm long, 0.7-1.0 mm wide, 7-11-veined; *sterile florets* staminate, rarely perfect, *lemma* 9-11-veined, *paleas* ¾ the length of fertile floret, *anthers* 1.8 mm long, sometimes rudimentary; *fertile florets* 3.0-3.5 mm long, 1.6-2.0 mm wide, ovate, black to brownish at maturity, *lemmas* upper margins not enrolled, *anthers* up to 2.0 mm long, usually yellowish, *stigmas* white; *caryopses* 2.3 mm long, 1.8 mm wide. *Chromosome number*: n = 18, $2n$ = 36 (Davidse 1972, 1978).

Iconographs

Fig. 107 (Pohl 1980); Fig. 98 (Davidse 2004).

Vernacular names

Belize: "*rat rice*" *P.H. Gentle 3632* (NY, US); **Brazil**: "*capim*" *R. de Lamos Froes 21119* (NY, US); **Colombia**: Boyaca, "*cañuela*" *Lawrance 795* (G, K, MO, US); "*cañuela trepadora*" (Quattrocchi 2006); **Costa Rica**: Alajuela, "*cañuela*" *Jiménez 532*, "*trompilla*" *Jiménez 886* (Davidse 1978); **El Salvador**: San Salvador, "*carrizo de cohetes*" *S. Calderón 849* (US), "*carrizo*" *P.C. Standley 23576* (US), "*carrizo de cohetera*" (Quattrocchi 2006); **Guatemala**: Huehuetenango, "*cañuela*" *J.A. Steyermark 49201* (F), Boyaca, "*cañuela*" *A.E. Lawrence 795* (G, K, MO, US), Izabal, "*cola de venado*" *S.F. Blake 7836* (US); **Mexico**: Chiapas "*zacatón*" *Chavelas & al. 1649* (Davidse 1978); Guerrero: "*akat*" *M. Jiménez & M.Gorostiza S. 31045* (US); Jalisco, "*carricillo*" *F.J. Santana M. & D. De Niz 5494* (US); Nayarit: Jalisco, "*otacillo*" *R.S. Ferris 5848* (US); Oaxaca, "*Am ay Carizo*" *S. Matthias & S. Geck 186* (G), "*cordoncilla*" *Chavelas & Perez 6* (Davidse 1978), Tabasco, "*zacate cenizo*" *Dioscoreas 11507* (Davidse 1978); "*carricillo*", "*carricillo de la sierra*" (Quattrocchi 2006); **Venezuela**: Anzoàtegui, "*pito-pito*" *J.A. Steyermark 61115* (US); Bolívar "*aré-ré-aketene*" *B. Boom & M. Grillo 6418* (MO, NY).

Ethnobotanical and economic uses

Colombia: Boyaca, "*Horse and cattle feed*" *A.E. Lawrence 795* [G, K, MO, US)]; **Guatemala**: Ixcan, "*decoction of leaves used for eyes diseases*" *J.A. Steyermark 4901* (F); **Mexico**: Oaxaca, "*decoction of stem, orally against urinary tract disorders*" *S. Matthias & S. Geck 186* (G); **Venezuela**: Anzoátequi, "*forage for domestic animals*" *J.A. Steyermark 61115* (US). Davidse (1978) reports its use for broom making in the Caribbean area.

Distribution

Belize, Brazil, Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Guyana, Honduras Mexico, Nicaragua, Panama, Perú, Venezuela. (Fig. 36).

Distribution (bibliographic references)

Hitchcock (1913, 1920, 1922, 1930); Standley and Calderón (1925); Schipp (1933); Standley (1937); Swallen

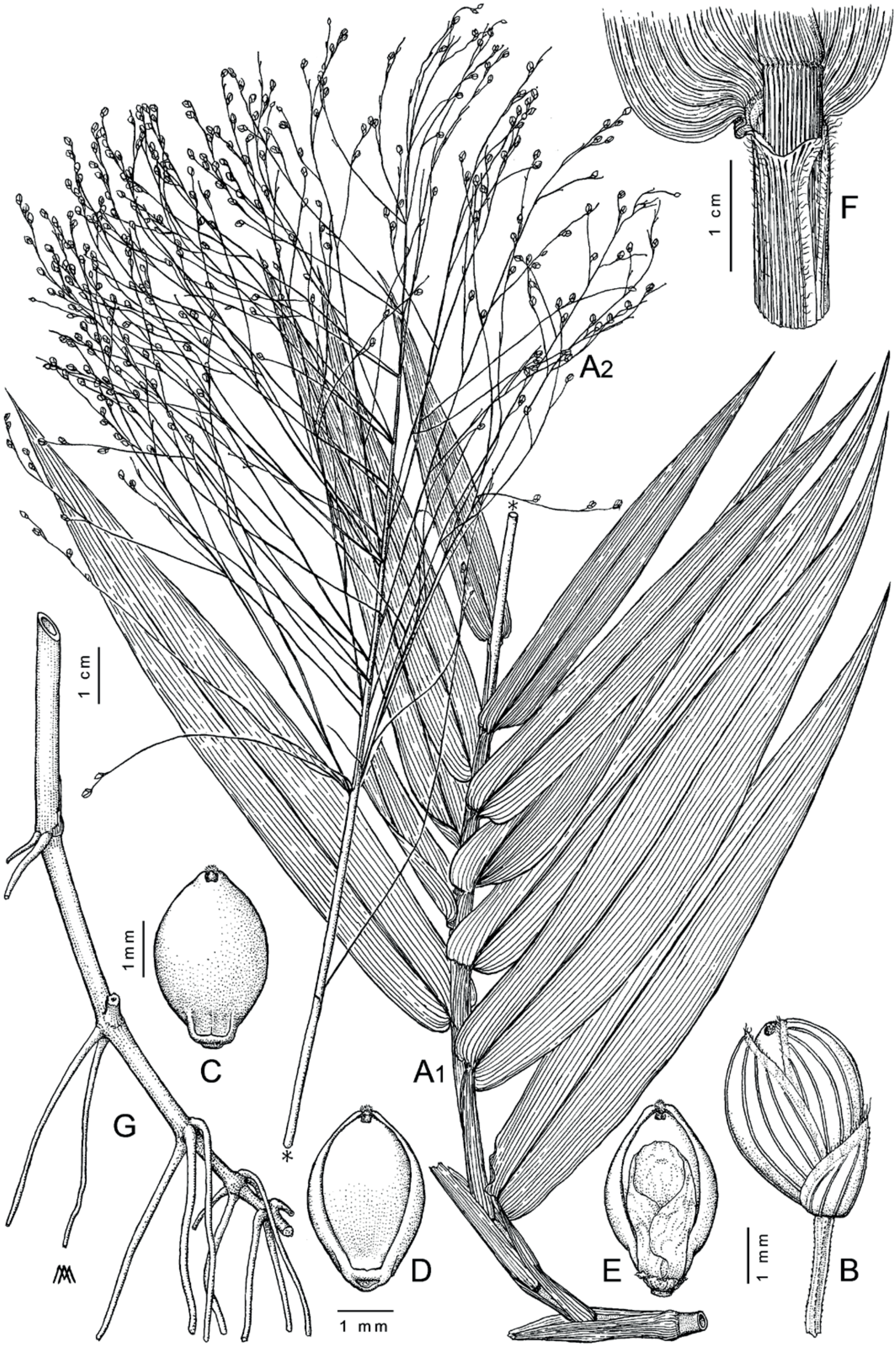

Figure 35. *Lasiacis procerrima* (Hack.) Hitchc.: **A1**. Habit at medium length with persistent leaf sheaths and blades cordate clasping; **B**. Erected spikelet lateral view; **C**. Fertile upper floret dorsal view; **D**. Fertile upper floret ventral view without lower persistent palea; **E**. Fertile upper floret ventral view with lower persistent palea. [A1-E. from C. *Whitefoord & C.A. Yacab 9331* (BM)]; **A2**. Apical part of the culm with dense fertile branches; **F**. Ligular area**. G.** Culm toward the base rooting at the nodes, and prop roots [A2 & G. from *G. Davidse 2161* (L)]. *A. Maury delineavit.*

Figure 36. *Lasiacis procerrima* (Steud.) Hitchc.: general geographic distribution.

(1931, 1936, 1943, 1955b); Beetle (1977); Davidse (1978, 1994, 2001, 2004); Croat (1978); Pohl (1980); McVaugh (1983); D'Arcy (1987); Judziewicz (1990); Zuloaga et al. (2003); Morales (2003); Hollowell et al. (2003); Correa et al. (2004); Renvoize et al. (2006); Davidse et al. (2007); Hokche et al. (2008); Sutherland (2008); Bono (2010); Giraldo-Cañas (2011); Dorr (2014); Villaseñor (2016); Dávila et al. (2018); Sánchez-Ken (2019); Menjivar et al. (2021).

Ecology

Roadsides and embankments, edges of secondary vegetation, open and disturbed areas, savannas, woodlands, and along trails in montane forests. Sea level up to 2400 m [Colombia: Magdalena (*W. Seifriz 165* (US)].

Phenology

June through January.

Remarks

Hackel (1901) cited the type collection as *H. Pittier 8819*, while isotypes at G and US bear labels "*Costa Rica, Buissons au bord du Tilirì prés La Verbena et Alajuelita, 1000 m, Aug. 1894, A. Tonduz 8819*".

L. procerrima is the most distinctive species in the genus, and rarely misinterpreted. Many herbarium specimens are still confused with *Stephostachys mertensii* (Roth) Zuloaga & Morrone (≡ *Panicum mertensii* Roth), as pointed out by Davidse (1978).

Lasiacis procerrima has mainly glabrous leaves, however, it is possible to find puberulent sheaths and densely pubescent blades in Mexico and other areas in Central America such as in Honduras (e.g., *G. Davidse & R.W. Pohl 2161* (K, L, NY, US) and in Panama (*G. MacPherson 11298* (MO, PMA). Culms can be tall up to 4-5 m (*G. Davidse 2910* (MO, NY, US) . The species is used by local people either as animal food, or for ethnomedical purposes.

The distribution is principally in Central America but the species ranges into South America in Colombia, Guyana, Venezuela, Ecuador, Peru, and northern Brazil.

Selected specimens

BELIZE. **Belize**. Gracie Rock, Sibun River, 2 Aug. 1935, *P.H. Gentle 1743* (K, NY, US); **Cayo**. Mountain Pine Ridge, San Agustin, Jul.-Aug. 1936, *C.L. Lundell 6571* (NY, US); Augustine, Mountain Pine Ridge, 1959, *D.R. Hunt 268* (US); Smokey Branch River, 14 May 1995, *C. Whitefoord & C.A.Yacab 9331* (BM); Along Hummingbird at mile 28, 26 Jun. 1973, *J.D. Dwyer 11416* (MO, NY); Chiquibil, Ceibo Grande, 700 m, 16°33'59"N, 89°05'52"W, 27 Aug. 1998, *S. Cafferty & A. Monro 33* (BM, MO); Ceibo Grande, 930 m, 16°31'25"N, 89°05'36"W, 9 Mar. 2000, *M. Peña & al. 1055* (MO); Maya Mountain divide in the vicinity of Doyle's Delight, the highest point in the Country, 900 m, 16°29'N, 89°04'W, 25 Aug. 2007, *B.K. Holst & al. 9069* (MO); **Stann Creek**. Stann Creek Valley, 8 Sep. 1938, *P.H. Gentle 2638* (K, NY); **Suchipéquez**. Mazatenango, Nov. 1870, *G. Bernoulli 1189* (K); s.l., 17 Jan 1931, *W.A. Schipp 785* (G, NY); **Toledo**. Monkey River, 8 Oct. 1941, *P.H. Gentle 3632* (NY, US); Blanden Nature Reserve, slopes above Blanden River, E and N of Solomon Camp, 16°32'N, 88°45'W, 4 Aug. 1995, *D. Atha & al. 1245* (MO, NY) .

BRAZIL. Brasilia, s.d., *L. Riedel 1239* (FI); **Amazonas**. Amazonas, São Gabriel, Río Negro, 23 Feb. 1944, *J.T. Baldwin 3538* (US); Amazonas, São Gabriel, Río Negro, base da Serra de São Gabriel, 8 Oct. 1945, *R. de Lemos Fróes 21119* (NY, US); Río Negro, Serra de S. Gabriel, 2 May 1948, *G.A. Black 48-2495* (US); Río Negro, road from Tapuruquara to airport, 25 Oct. 1971, *G.T. Prance & al. 15832* (NY, US); **Roraima**. Serra dos Surucucus, S of Mission Station, 2°42'N, 63°33'W, 18 Feb. 1969, *G.T. Prance & al. 10052* (MO, NY, US).

COLOMBIA. **Antioquia**. Malena, 12 Jan. 1918, *F.W. Pennell 3777* (NY, US); Carretera al mar en los alrededores del Río Ampurrumiadó, 200 m, 11 Oct. 1947, *G. Gutierrez & F.A. Barkley 170145* (US); Remedios, Sitio Otú, 3 km del Corregimiento Santa Isabel, Vereda Los Lagos, 820 m, 74°45'W, 6°56'N, 14 Jul. 1987, *J. Callejas & al.* 4728 (K, MO, NY, US); Puerto Berrio, margen izquierda de la quebrada "Malena", 170-200 m, 20 Oct. 1999, *R. Fonnegra & al. 6954* (MO); **Boyuca**. El Humbo, 130 miles N of Bogotá, 3000 ft, 11 May 1933, *A.E. Lawrence 795* (G, K, MO, US); **Caquetá**. Morelia, Verda de Santander, quebrada of Río Bodoquero (between Río Pescado and Río Guecochará), 430 m, 20 Jan. 1969, *T.R. Soderstrom 1402* (US); El Recluta, 10 km north of Florencia along road to Neiva, 22 Jan. 1969, *T.C. Plowman & H. Kennedy 2246* (US); 23 km N of Florencia along main road to Garzon, E slope of Eastern Cordillera, 560 m, 12 Jan. 1974, *G. Davidse & al. 5764* (MO, US); Km 26.7 via Florencia-Guadalupe, 10 Feb. 1987, *X. Londoño & I.D. Quintero 145* (US); **Chocó**. Río San Juan just below Tado, 100 m, wet forest, 15 Aug. 1976, *A. Gentry & M. Fallen 17724* (MO); **Cordoba**. Carretera Tierralta-Frasquillo, 5 km en la desviacion a Chibogadò, 250 m, 23 Jul. 1986, *R. Bernal & al. 1127* (MO, NY); **Cundinamarca**. Icononzo, 1-4 Dec. 1917, *F.W. Pennell 2870* (NY); 20 km NW of Villavicencio, along the road to Bogotá, 800 m, 3 Jan. 1974, *G. Davidse & F. Llanos 5523* (K, US), **n = 18!** (Davidse 1978); **Huila**. E of Neiva, 31 Jul. 1917, *H.H. Rusby & F.W. Pennell 516* (NY); **Magdalena**. Santa Marta, Jul. 1903, *H.H. Smith 117* (G, K, MO, NY, P, US); Cordillera de Santa Marta, S. Andrés de La Sierra, 12 Jul. 1906, *H. Pittier 1645* (US); Magdalena Valley, near Lake Sapatora, Rincon Hondo, 9 Aug. 1924, *P.H. Allen 367* (K, MO); Mt. San Lorenzo, near Santa Marta, 1900-2400 m, Jul. 1932, *W. Seifriz 165* (US); Parque Nacional Sierra Nevada de Santa Marta, Cuchilla de San Lorenzo, headwaters of Río Guachacas, 1300 m, 14 Jul. 1989, *X. Londoño & L. Clark 459* (MO); Alto Río Frio, Cabeceras del Río Congo, Ciudad Antigua, por el camino al Alto del Chimborazo, 1100-1200 m, 10°59'N, 74°04'W, 26 Jul. 1989, *S. Madriñan & C.E. Barbosa 513* (MO); **Meta**.Villavicencio to Buenavista, 4 Sep. 1917, *F.W. Pennell 1648* (NY); Meta, near Villavicencio, 500 m, 18-19 Mar. 1939, *E.P. Killip 34505* (BM, US); Llanos de San Martín, Guamal, orillas del Río Humadea, 500 m, 10 Sep. 1958, *R. Jaramillo-Mejía & al. 1019* (MA, US); Sierra de La Macarena, Río Guapaya, 30 Nov. 1949, *Philipson & al. 1651* (BM); San Juan de Arama, 26 Feb. 1969, *G. Pinto & C. Sastre 1105* (P); Sierra de La Macarena, Vereda El Tablazo, a orilla del Caño Diamante, afluente del Río Güjar, 550 m, 29 May 1973, *M.L. Chaparro & al. 107* (MO); Guayabetal-Villavicencio, 10 Jun. 1983, *J.R. Wood 3801* (K); In the Río Guatiqua, ca. 5 km above Villavicencio, 26 Feb. 1984, *J.R. Wood 4260* (K); Restrepo, Salinas, 600-700 m, 12 Jun. 1989, *F. Zuloaga 3933* (US); Mesetas, 450 m, 74°15.5'W,3°8.2'N, 11 Aug. 1989, *J. Betancur 1341* (MO, NY); **Valle**. Santa Rosa to Cisneros, Dagua Valley, 250-350 m, 10 May 1922, *E.P. Killip 5366* (NY, US); Santa Rosa, Dagua Valley, 200-300 m, 22 Sep. 1922, *E.P. Killip 11564* (US); Dagua, Buenaventura, 540 m, 6 Feb. 1961, *J.M. Idrobo 4274* (US); Valle, Dagua, corregimiento El Danubio, Alto Anchicayá, 200 m, 19 Jun. 1984, *W. Devia A. 579* (MO); **Vaupés**. Mitú and vicinity, along lower Río Kuduyarí, 26 Jun. 1976, *J.L. Zarucchi 1739* (K, MO, US).

COSTA RICA. **Alajuela**. Cerro de Espiritu Santo, 1-3 km SW of Naranjo, 2 Sep. 1966, *A.S. Weston 2099* (US); Cordillera Central, along road between Puerto Viejo and San José, 760 m, 10°18'N, 84°11'W, 28 Sep. 1987, *T.B. Croat 68210* (MO); Cantón de San Ramón, Cord. de Tilarán, 10°13'00"N, 84°37'00"W, 800-850 m, 27 Aug. 1995, *J. Gomez Laurito 12813* (USJ); **Cartago**. Turrialba, 23 Jul. 1949, *J. Léon 1702* (US); Turrialba, 600 m, 18 Aug. 1966, *R.W. Pohl & C. Calderón 10356* (USJ); 18 km N of Turrialba, 6 Aug. 1968, *R.W. Pohl & G. Davidse 10824* (K, US); Turrialba, Capote, 29 Jun. 1976, *J. Gomez Laurito 1703* (USJ); Turrialba, camino a Siquirres, Pavones, 21 Aug. 1977, *J. Gomez Laurito 3049* (USJ); Cartago, La Unión, Dulce Nombre de Tres Ríos, 2000 m, 18 Oct. 2004, *G. Barrantes s.n.* (USJ); **Guanacaste**. 10 km NE of Las Juntas, 19 Aug. 1968, *R.W. Pohl & G. Davidse 10960* (C, K, US) **n = 18!** (Davidse 1978); Vicinity of Cañas, 12 Dec. 1969, *R. Daubennire 399* (USJ); Camino de entrada al Parque Nacional Sta. Rosa, 12 Oct. 1974, *J. Gomez Laurito 262* (USJ); Santa Rosa National Park, 30 km NW of Liberia, 300 m, 10°50'N, 85°35'W, 27 Jan. 1985, *D.H. Janzen 12426* (MO); La Cruz, P.N. Guanacaste, Volcàn Orosì, 9 km S de Santa Cecilia, 700 m, 10°59'25"N, 85°25'37"W, 14 Jul. 1997, *C. Moraga & P. Rios 914* (MO, NY); La Cruz, P.N. Santa Rosa, Golfo de Papagayo, Sector Murcielago, Paya Blanca, Bosques de galeria aguas Arriba de la Quebrada Grande, 100 m, 10°51'24"N, 85°55'09"W, 13 Jan. 2003, *J. González & al. 2576* (MO); **Heredia**. About 35 km NE of Alajuela, 18 Aug. 1967, *R.J. Taylor 4520* (MO, NY); Heredia-San José, Río Virilla, 4 km N of San José, 22 Sep. 1971, *R.W. Lent 2154* (NY); **Limón**. 4 km SW of Río Hondo, 11 Jul. 1966, *T.R. Soderstrom & al. 1212* (US); 6 km W of Guapiles, wooded hills E and W of bridge over Río Toro Amarillo, 9 Jul. 1966, *R.W. Pohl & C. Calderón 10016* (MO); 1 km SW of Pueblo Nuevo, 17 Sep. 1968, *R.W. Pohl 11096* (K, US); Cimarrones, ca. 10 km E of Siquirres, 5 Aug. 1974, *P.J.M. Maas 1132* (K); **Puntarenas**. 26 Oct. 1911, *A.S. Hitchcock 8572* (US); Along road from Boruca to the Carretera Interamericana, 22 Aug. 1968, *R.W. Pohl & al. 10993* (K, US); 2 km NE of Escuela Santa Constanza, N of San Vito de

Java, 27 Sep. 1968, *R.W. Pohl 11163* (K, US) **n = 18!** (Davidse 1978); **San José**. El General, Valle du Diquis, 700 m, 3 Feb. 1898, *H. Pittier 12057* (BR, P, US); Vicinity of El General, Dec. 1935, *A.F. Skutch 2167* (BM, K, MO, NY, US); El General Valley, vicinity of San Isidro El General, 2 Mar. 1966, *A. Molina & al. 18221* (NY, US); Along Río Conejo in the Valley of the Río Al Umbre, 6 Sep. 1968, *R.W. Pohl & al. 11055* (K, US); Cantón de Mora, Zona Protectora El Rodeo, Rserva de la Universidad para la Paz, bosque humedo montano, 850-900 m, 09°54'20"N, 84°16'30"W, 11 Aug. 1998, *A. Cascante 1436* (USJ); Tarrazu, Estribaciones del Cerro Diamante, 09°32'30"N, 84°01'20"W, 700 m, 24 Sep. 1998, *A. Estrada 1783* (USJ); Acosta, Cuenca del Pirrís-Damas, Acosta, Colorado, Filia San Jrónimo, Río Colorado, 16 Oct. 2000, *J. Morales 7382* (G); Puriscal, Cuenca del Pirrís-Damas, Concepcion, a orillas del camino, 28 Apr. 2001, *Bustamante 35* (G); Acosta, Cuenca del Pirris-Damas, Acosta, Fila San Jeronimo, camino a Fila Pital, por Quebrada San Jeronimo, 300-1100 m, 9°41'30"N, 84°12'50"W, 9 May 2004, *J. Morales 10597* (MO).

ECUADOR. **Napo**. On the road from Napo to Puyo, 600 m, 10 Dec. 1970, *H. Ellenberg 290* (MO); **Pastaza**. ca 40 km along road towards Arajuno, 01°57'S, 77°52'W, 19 Sep. 1998, *S. Lægaard 19171* (K), *19172* (MO).

EL SALVADOR. **Ahuachapán**. San Benito, San Alfonso, 12 Aug. 1994, *Chinchilla Peña & al. ISB00584* (K); **Chalatenango**. Pass 7 km SSE of La Palma along Highway 4, 1050 m, 11 Jun. 1970, *G. Davidse & R.W. Pohl 2072* (MO), **n = 18!** (Davidse 1978); **Morazán**. About 4 km E of finca of General J.T. Calderón, Montes de Cacaguatique, 12 Jan. 1942, *J.M. Tucker 777* (K, US); **Morazán**. A.P. Río Sapo, cuenca de Río Talchiga, 700 m, 13°55'N, 88°6'W, 6 Feb. 2004, *R.A. Carballo 1042* (MO); **Santa Ana**. Parque Nacional Montecristo, 14°23'22"N, 89°23'15"W, 1416 m, 10 Feb. 2016, *J. Menjívar & R.M. Baldini 3482* (FT, MHES); **San Salvador**. 1922, *S. Calderón 849* (NY); San Salvador, vicinity of Ayutuxtepeque, 3 Feb. 1922, *P.C. Standley 20512* (US); Vicinity of San Salvador, Mar. 1922, P.*C. Standley 23576* (US).

GUATEMALA. **Alta Verapaz**. Alta Verapaz, Cubilgüitz, Oct. 1906, *H. von Türckheim 1028* (G, L, MO, US); Cubilquitz, 1906, *H. von Türckheim 8781* (FI, L, US); 1841, *E. Ritter von Friedrichsthal 549* (FI); **Guatemala**. Guatemala City, 1-3 Dec. 1911, *A.S. Hitchcock 9067* (US); Guatemala, 10 km S of San Raimundo, 18 Jan. 1939, *P.C. Standley 62914* (NY); **Huehuetenango**. Around Ixcan at "Patcushín", Sierra de los Cuchumanates, 500 m, 22 Jul. 1942, *J.A. Steyermark 49201* (F); Malpais, orilla del camino, Barillas, 1250 m, 15°51'31"N, 91°13'40"W, 22 Sep. 2006, *Dasa 4911* (MO); **Izabal.** Bank along shore of Lake Izabal, 1 Jun. 1919, *S.F. Blake 7836* (US); Vicinity of Quiriguà, 15-31 May 1922, *P.C. Standley 24244* (NY, US); Slopes WNW of (above) El Estor, along margin of open pit nickel mine, 410 m, 30 Aug. 1988, *W.D. Stevens & E. Martinez S. 25234* (MO); El Estor, 10 Nov. 2005, *F. Ramirez & M. Cano 1570* (MO); **Quezaltenango**. Colomba, 24 Sep. 1934, *A.F. Skutch 1298* (US); **San Marcos**. Near San Rafael, 600 m, 11 Jul. 1977, *T.B. Croat 40779* (MO); **Santa Rosa**. Mar. 1892, *J.D. Smith 3906* (US); Santa Rosa, Cenaguilla, Sep. 1892, *E.T. Heyde & Lux 3906* (BM, US); Between Taxisco and Guazacapán, 3 Dec. 1940, *P.C. Standley 79136* (K); **Zacapa**. Between Santa Rosalia and first waterfall, 1200-1500 m, 9 Jun. 1942, *J.A. Steyermark 42250* (F, US).

GUYANA. **Potaro-Siparuni**. Kaieteur Savannah, 1881, *G.S. Jenman 813* (US); Kaieteur Savannah, 1200 ft, 3 Sep. 1937, *N.Y. Sandwith 1322* (NY, US); Southern Pakaraima Mts., Kamanà Falls, 25 Aug. 1961, *B. Maguire & al. 45951A* (NY); Kaieteur Plateau, vicinity of Kaieteur Falls and along western rim of Potaro Gorge, 1400 ft, 18 Feb. 1962, *R.S. Cowan & T.R. Soderstrom 1889* (C, NY, US); Kaieteur Falls National Park, along rim downstream from the falls, 500 m, 5°10'N, 59°29'W, 13 Apr. 1988, *W. Hahn 4520* (US); Approx. 1 km N of Kato, along trail to Paramakatoi, 750 m, 4°40'N, 59°55'W, 14 Mar. 1989, *W. Hahn 5715* (CAY, NY, US); 2-3 km N of Kato Village store-airstrip, along trail off Kato-Kurukabaru road, 690-750 m, 4°41'N, 59°48'W, 17 Mar. 1989, *L.J. Gillespie 866* (CAY, US).

HONDURAS. **Atlantida**. About 15 miles E of Ceiba, 21 Jul. 1938, *T.G. Yuncker 8594* (NY); **Colón**. Bario Central Trujillo, 9 Nov. 1980, *J. Saunders 700* (NY); Sacate, Cerro Calentura, 3 km SE de Trujillo Colón, 29 Sep. 1989, *D. Clarke 30* (BM); **Comayagua**. Near El Achote, above the plains of Siguatepeque, 15 Jul. 1936, *T.G. Yuncher & al. 5898* (G, NY, US); **Gracias a Dios**. La Mosquitia, 17-21 Jul. 1977, *C. Nelson & Romero 4182* (BM); **Lempira**. Along trail from old electricity generation plant to Camp Don Tomas, ca. 10 straight line WSW of Gracias Parque Nacional Celaque, 1850 m, 14°33'N, 88°40'W, 11 Feb. 1993, *R. Evans 1163A* (MO); **Morazán**. Santa Clara, 23 Aug. 1946, *L.O. Williams & A. Molina 10408* (US); San Antonio del Oriente, 20-21 Oct. 1951, *J.R. Swallen 10970* (US); Foothills of Mt. Uyuca beyond Las Floras, 4 Nov. 1951, *J.R. Swallen 11303* (US); 8 km E of El Zamorano, 14 Jun. 1970, *G. Davidse & R.W. Pohl 2081* (MO, NY, US); Between El Zamorano and San Antonio de Oriente, 21 Jun. 1970, *G. Davidse & R.W. Pohl 2161* (K, L, NY, US); **Yoro**. Cerro between Río Guan Guan and Río Texiguat, E of Cerro Guan Guan, S of San José in the Río Lean Valley, W end of the Cordillera de Nombre de Dios, 700-870 m, 15°29'30"N, 87°27'00"W, 6 Nov. 1988, *J.M. McDougal & al. 3240* (MO).

MEXICO. **Chiapas**. 10 km S of Pueblo Nuevo Solist, 28 Jul. 1965, *E. Lathrop 6006* (US); Tabasco border, 33 km S of Sureste on road to Mal Paso, 17°25'N, 93°35'W, 23 Aug. 1965, *K. Roe & al. 1367* (US); Tenejapa, in the paraje of Mahosik', 28 Nov. 1966, *A.S. Ton 1653* (NY); Simojovel de Allende, along the road from El Bosque to Simojovel, 10 Oct. 1967, *A.S. Ton 3077* (NY); Ocozocoautla de Espinosa, SW side of the Presa de Malpaso, 5 Dec. 1967, *A.S. Ton 3294* (US); Villa Corzo, at the E base of Cerro Tres Picos near Cerro Bola, 9 Feb. 1972, *D.E. Breedlove 24080* (MO, NY); Motozintla, Belisario Dominguez, 19 Nov. 1977, *J.I. Calzada & al. 3964* (NY); Ixtapa, carretera Tuxtla Gutierrez-Pichucalco, 28 Dec. 1984, *C. Cowan 5047* (NY); Road from Tuxtla Gutierrez to Ixtapa, 31 Jan. 1990, *P.J. Stafford & al. 154* (BM); La Concordia, Finca Custepec, c. 1180 m, 15°44'N, 92°58'W, 12 Jul. 1990, *R.J. Hampshire & al. 1267A* (BM, MA); Ocosingo, a 5 km de San Javier, al S del crucero, 387 m, 16°46'N, 91°06'W, 14 Sep. 2002, *G. Aguilar M. 2799* (MO); Villacorzo, Zona Nucleo Cerro Bola, 1700 m, 16°08'N, 93°35'W, 14 Jul. 2004, *A. Reyes-Garcia 7284* (MO); **Durango**. Road to Durango, 1.8 miles W of La Guayanerga, 30 Sep. 1971, *D. Jackson 134* (NY); **Guerrero**. Road between Acahuizotla and Agua de Obispo on Highway to Acapulco, 1 Oct. 1949, *H.E. Moore Jr. 5149* (BM, G, US); Guerrero 10 miles N of Taxco, 6 Sep. 1959, *O. Degener & I. Degener 26290* (NY); E of El Aguacate, km 88 on Mexico 51 Iguala to Arcelia, 17 km by air WNW of Teleopan, 1500 m, 18°23'N, 100°01'W, 23 Sep. 1977, *H.H. Iltis & J.F. Doebley 349* (MO); Cuauhtémoc, Puebla, en un lugar llamado Totoapan, 21 Oct. 2015, *M. Jiménez & M.Gorostiza S. 31045* (US); **Jalisco**. Río Blanco, Oct. 1886, *E. Palmer 535* (K, MO, NY, P, UPS, US); Near Guadalajara, 30 Oct. 1888, *C.G. Pringle 1732* (BM, G, K, MO, NY, P, US, W); Michoacan et Guerrero, El Ocote, Cerro Pedregoso, 29 Oct. 1898, *E. Langlassé 540* (G, K, P, US); Barranca de Guadalajara, 25 Oct. 1903, *C.G. Pringle 11760* (K, L, US); 8 miles W of Guadalajara, 13 Sep. 1959, *T.R. Soderstrom 611* (US); 4 miles NNE of Talpa de Allende, 12-13 Oct. 1960, *R.*

McVaugh 20155 (NY, US); Tamazula, cerca de Agua Hedionda, ca. 45 km al E de El Aserradero, 26-27 Oct. 1973, *R. McVaugh 21152* (NY); Along road to San Cristobal de la Barranca, 2 Nov. 1975, *P.M. Peterson 371* (K); Villa Guerrero, 25 Sep. 1980, *A.A. Beetle 5790* (MO); Zapolitlan, East side of Lago La Maria, 22 km NNW of Colima in the SW foothills of the Volcán de Colima, 1250 m, 19°27.6'N, 103°42.5'W, 7 Jan. 1991, *A.C. Sanders 10349* (MO, US); Autlán, 11-12 km al S de Autlán, 2 km al SW de Ahuacapán, 1500 m, 3 Oct. 1991, *F.J. Santana M. & D. De Niz 5494* (US); 8 km al W de Xalisco, camino de terraceria de Xalisco al Malinal, bosque de *Pinus-Quercus*, 21°25'56"N, 104°57'26"W, 1500 m, 16 Oct. 1994, *G. Flores-Franco 4007* (BR); **Michoacán**. Prope Uruapan, 22 Jan. 1926, *G.J.N. Woronow 2706* (US); Uruapan, near Zararacua Falls, 7 miles SW of Uruapan, 30 Jul. 1941, *C. Leavenworth 1255* (US); Road from Temascal to Huetamo, 13 Nov. 1949, *H.E. Moore Jr & al. 5697* (BM, G, US); On steep slopes of barrancas on road from Uruapan to Nueva Italia, 5 Oct. 1953, *E.R. Sohns 864* (K, US); West facing slopes of Cerro de Carboneras above the Río Cupatitzio, ca. 22 km S of Uruapan, 16-22 Oct. 1961, *R.M. King & T.R. Soderstrom 4802* (NY, US); **Nayarit**. Vicinity of Jalisco, 8 Nov. 1925, *R.S. Ferris 5848* (US); Trail from Tepic to Santiago, 15 Sep. 1926, *Y. Mexia 628* (MO, NY, US); About 10 road-miles E of Jalcocotán, on road to Tepic, 4 Oct. 1952, *R. McVaugh 13357* (K, US); Nayarit, 9 miles N of Compostela, 12 Nov. 1959, *R. McVaugh & W.N. Koeltz 500* (US); 2 miles W of Mazatan, 17 Sep. 1960, *R. McVaugh 19101* (NY, US); Valle de Banderas, 1 km N de El Cuatante, 17 Nov. 1963, *J. Rzedowski 17844* (US); Nayar Cerro Cangrejo, camino de Herradura a El Cañaveral y/o a Jesus Maria, 1200-1400 m, 22°15'N, 104°37'W, 17 Sep. 1989, *P. Tenorio 16092* (MO); Xalisco, 4 km del camino de terraciera de Xalisco a la Estación de Microondas Cerro Boludo, 21°27'N, 104°56'W, 3 Oct. 1993, *O. Tellez & al. 12998* (US); Tepic, 10 km al E de la Yerba, carretera La Yerba-Tepic o al SE de la desviacion La Peñita, bosque de *Pinus-Quercus*, 21°31'20"N, 105°00'57"W, 945 m, 15 Sep. 1994, *G. Flores-Franco 3673* (BR); **Oaxaca**. Tuxtepec, Chiltepec and vicinity, Jul. 1940-Feb. 1941, *G. Martinez-Calderon 239* (US); Ixtlan-Tuxtepec road, 21-23 km S of Valle Nacional, 26 Jul. 1964, *J.T. Mickel 1463, 1485* (NY); San Juan Guichicovi, carretera a Uxpanapa, 3 km al E de Sarabia, 12 Nov. 1978, *S.D. Koch & al. 78235* (NY); Ixtlan, Comaltepec, La Esperanza, 1600 m, 17°37'N, 96°21'W, 2 Aug. 1988, *R. López Luna 338* (MO); Santa Maria Chimalapa, on gravel along road 2 km from Escolapa towards El Mezquite, 16°50'02.3"N, 94°45'30.6"W, 220 m, 5 Aug. 2014, *S. Matthias & S. Geck 186* (G); **Orizaba**. 1866, *E. Bourgeau 2971* (L, P); **Puebla**. Nauzontla, 20°01'N, 97°38'W, 6 May 1989, *P. Tenorio 15802* (NY); **San Luis de Potosí**. 1878, *C.C. Parry & E. Palmer 535* (BM); **Sinaloa**. S. Ignacio, Valley of Río Piaxtla, Nov. 1917, *A.E. Salazar 31* (US); Cerro Colorado, 5 Dec. 1939, *H.S. Gentry 5126* (MO, NY, US); 16 miles NE of Concordia, 18 Oct. 1966, *F.W. Gould 12250* (US); Along the dirt road from Rosario to Plomosas, 7 Oct. 1975, *J.L. Reveal & R.M. Harley 4043* (K, US); Concordia, km 228 from Durango on the Mazatlan to Durango road, 1 Oct. 1985, *B. Bartholomew 2538* (MO, NY); Concordia, El Capomito, Ejido Los Ciruelos, 23°18'10"N, 105°56'12"W, 7 Jan. 2006, *A.L. Reina & al. 124* (US); **Temascaltepec**. Rincón del Carmen, 1 Oct. 1932, *G.B. Hinton 1948* (BM, K, MO, NY); Temascaltepec, Temascaltepec, 15 Nov. 1932, *G.B. Hinton 2408* (K, NY, US); **Veracruz**. Mirador, Jul. 1838, *J.J. Linden 72* (FI-Webb, G); 1840, *H. Galeotti 5717* (G, NY, P, US, W); Mirador, 1841-43, *F.M. Liebmann 14195* (C, US); Orizaba, Aug. 1910, *A.S. Hitchcock 6385* (L, US); Córdoba, Aug. 1910, *A.S. Hitchcock 6422* (BM, G, K, L, MO, NY, P, US, W); Zacuapan, Dec. 1916, *C.A. Purpus 7813* (MO, NY, US); La Barranca de las Flores, about 10 km W of Cordoba, 23 Aug. 1943, *J.V. Santos 2500* (US); Along trail leading to base of the large tropical Teocello Canyon, near Teocello, 25 Aug. 1959, *T.R. Soderstrom 469* (US); Las Chiapas, Ceiba Blanca, 25 Oct. 1973, *J. Dorantes & al. 2261* (NY); Tlacapoyan, about 6 km (by air) S of Tlapacoyan on road to Altolonga, 800 m, 19°55'N, 97°13'W, 11 Jul. 1982, *M. Nee & G. Giggs 24870* (MO).

NICARAGUA. **Atlantico Nord.** Río Leicus, la Tronquera, SW de Waspan, 18 Aug. 1965, *A. Molina 14904* (NY); **Carazo**. Jinotepe, 3-7 Nov. 1911, *A.S. Hitchcock 8694* (US); **Chontales**. E of El Narajal, between Juigalpa and La Libertad, 500 m, 12°11'N, 85°15'W, 6 Aug. 1983, *W.D. Stevens 22444* (MO); **Estelí**. N slope of Cerro El Fraile, 1160-1200 m, 13°25'N, 86°15'W, 28 Sep. 1980, *W.D. Stevens & al. 18061* (MO); **Jinotega**. Wiwili, Comunidad La Esperanza, Reserva Bosawas, Territorio Miskito Indian Tasbabay Kum, parcela 1, 1 km al oeste de la finca de Leonidas Bodin, 60-70 m, 14°23'02"N, 85°32'09"W, 7 Sep. 2007, *D. Prado G. 95* (MO); **León**. San Nicolas, El Barro, 5 km al SE de San Nicolas, 1200 m, 12°55'N, 86°18'W, 12 Jan. 1984, *P.P. Moreno 22726* (MO); **Matagalpa**. El Ocotal, 4 km al S de la ciudad, 900-1000 m, 12°52'N, 85°55'W, 5 Oct. 1982, *P.P. Moreno 17704* (MO); **Nueva Segovia**. Jalapa, Cerro de Jesus, 1133 m, 13°56'51"N, 86°08'26"W, 14 Sep. 2010, *I. Coronado & al. 5488* (MO); **Río San Juan**. El Castillo, Reserva Indio-Maiz, Cerro El Diablo, 350-609 m, 11°01'N, 84°12'W, 9 Dec. 1998, *R. Rueda & al. 9639* (MO); Río San Juan, San Carlos, Reserva Esperanza Verde, 60 m, 11°04'N, 84°44'W, 15 Sep. 2001, *R. Rueda & al. 16543* (MO); **Zelaya**. Intersection of road to Puerto Cabezas-Waspan & Río Lecus, 14 Jul. 1970, *G. Davidse & R.W. Pohl 2347* (MO, NY, US), **n = 18!** (Davidse 1978); Zelaya, W of Bluefields, 3 Mar. 1971, *J.T. Atwood 4182* (NY); Zelaya, Monkey Point, 5 m, 11°35'N, 83°39'W, 20 Oct. 1981, *P.P. Moreno & J.C. Sandino 11935* (MO).

PANAMA. **Chiriquí**. 4.1 miles from Boquete on the road to David, 6 Aug. 1967, *J.H. Kirkbride 90* (MO, NY, SCZ); Chiriquí, Llanos Francia, ca. 400 feet, 19 Jul. 1968, *J.D. Dwyer & Lallathin 8724* (MO, SCZ); Chiriquí, along road in vicinity of branch in road to Cerro Colorado and Escopeta, above Río San Felix near town of San Felix, ca. 13 miles N of Río San Felix bridge), 800-1200 m, 15 Mar. 1976, *T.B. Croat 33410* (MO); Chiriquí, NO del campamento de Fortuna (Hornito), sitio de presa, 1000-1200 m, 12 Aug. 1976, *M. Correa & al. 2262* (FT, MO, PMA); Chiriquí, vicinity of Gualaca ca. 10.7 miles from Planes de Hornito, 11 Jul. 1980, *T. Antonio 5145* (BM, MO); Chiriquí, Orillas de la carretera Dolega-Boquete, 8°39'17"N, 86°26'24"W, 902 m, 24 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 902* (FT, PMA, SCZ); **Coclé**. El Valle, ca. 2500 ft, 27 Aug. 1961, *J.D. Dwyer 1820* (MO); About 8 miles north of El Vallé de Antón, 2 Aug. 1970, *J.L. Luteyn & H. Kennedy 1687* (F); Road from El Valle to La Mesa, 2600 ft, 10 Aug. 1971, *D. Spellman & al. 559* (MO); Area surrounding Rivera Sawmill, 7 km N of El Copé, 750-850 m, 24 Nov. 1977, *J.P. Folsom & L. Collins 6431* (MO); Parque Nacional Omar Torrijos Herrera, 8°39'49"N, 80°35'28"W, 758 m, 17 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 841* (FT, SCZ); **Colón**. Near Old Fort Lorenzo, mouth of Río Chagres, 8 Mar. 1923, *C.V. Piper 5948* (US); Maria Chiquita, E of Río Piedras toward Portobello, 9 Aug. 1967, *J.D. Dwyer & J.H. Kirkbride 7800* (MO); Donoso, camino a quebrada Canoa, 11 Jul. 1996, *J. Polanco & al. 2013* (PMA); Colón, Quebrada Nicaragua, Coclé del Norte, UTM 981643N, 565216E, 25 m, *J. Mendieta 689* (PMA); Colón, Santa Maria, El Guacimo. UTM 987432N, 576939E, 140 m, 15 Oct. 2001, *J. Mendieta 927* (PMA); Lago Gatún, Ciricito, UTM 996639N, 600658E, 40 m, *J. Mendieta 531* (PMA); Orillas de la carretera Portobelo-Nombres de Dios, 933'33"N, 79°34'33"W, 40 m, 29 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 919, 920* (FT, PMA, SCZ); **Darién**. Cana and vicinity, 1908, *R.S. Williams 773* (NY); Gold mine at Cana, 480 m, 26 Jul. 1976, *G.A. Sullivan 634* (MO); Río Cocalito, 9 Feb. 1982, *C. Whitefoord & A. Eddy 114* (BM); S of El Real, region called Alturas de Nique, near Cana mine, 550 m, 7°45'N, 77°40'W, 20 Aug. 1987, *G. McPherson 11499* (MO); **Herrera**. Carretera Chepo-Las Minas, sea level, 8°2'N, 80°29'W, 30 Sep. 1994, *C. Galdames 1811* (PMA); **Panamá**. Between Pedro Miguel and Corozal, 30 Aug. 1911, *A.S. Hitchcock 7961* (US); Canal Zone, between Frijolea and Bohio, 13 Oct. 1911, *A.S. Hitchcock 8393* (K, NY, US); Between Corozal and Ancon, 7 Sep. 1914, *H. Pittier 6774* (US); Canal Zone, W side of Canal opposite to Balboa, 7 Sep. 1920, *W.W. Rowlee & H.E. Stork 945* (NY, US); Ancon Hill, 17 Oct. 1922, *E.P. Killip 12066* (US); Taboga Island, Dec. 1923, *P.C. Standley 27055* (US); Barro Colorado Island, 4 Dec. 1931, *O. Shattuck 528* (STRI); Vicinity of Arenoso, lower Río Trinidad, 7-10 Aug. 1935, *R.J. Seibert 628* (K, MO, NY, US); Panamá, near Arraijàn, 21 Jul. 1938, *R.E. Woodson Jr. & al. 1399* (MO, NY, US); Isla Toboga, 23-24 Jul. 1938, *R.E. Woodson Jr. & al. 1453* (NY, US); Canal Zone, 18 Jan. 1940, *F.W. Hunnewell 16394* (NY); San José Island, about 55 miles SSE of Balboa, 10 Nov. 1944, *I.M. Johnston 442* (P, US); San José Island, Pearl Archipelago, 26 Jun. 1945, *C.O. Erlanson 383* (NY, US); Toward top of Cerro Campana, along road, 22 Oct. 1962, *J.A. Duke 5959* (MO); Fort Clayton, Chiva Chiva Trail near Miraflores Lake, 30 Sep. 1965, *E.L. Tyson 1378* (SCZ); 5 miles N Cerro Azul on road to Cerro Jefe, 13 Nov. 1965, *K.E. Blum & al. 1734* (US); Fort Clayton, 10 km SW of Canazas, 15 Apr. 1966, *J.S. McCorkle 199* (US); Canal Zone, Fort Sherman on Pena Road, 13 Oct. 1965, *E.L. Tyson & al. 1689* (PMA); Altos del Río Pacora, 2500 ft, 9 Jun. 1967, *W.H. Lewis & al. 2301* (MO); Canal Zone, Barro Colorado Island, E of Slothia Isle, 16 Sep. 1968, *T.B. Croat 6108* (MO, NY, SCZ); 1.5 miles above Interamerican Highway on road to Cerro Campana, 10 Sep. 1970, *T.B. Croat 12037* (MO, NY); Canal Zone, Frijoles, near end of Sniffer Road, spur of Pipeline Road, 21 Nov. 1970, *R. Foster 2026* (MO, PMA); Canal Zone, pipeline road app. 12 miles N of Gamboa, 1 Sep. 1972, *E.L. Tyson 6656* (MO); Panamá, E side of Cerro Campana, 8 Sep. 1973, *M. Nee 6870* (MO, NY); Canal Zone, Summit Gardens, 12 Oct. 1973, *M. Nee 7386* (K, MO, PMA); Canal Zone, secondary tropical moist forest at top of Cerro Pelado, 1 km N of Gamboa, 200-220 m, 3 Nov. 1973, *M. Nee 7766* (MO, PMA); Canal Zone, at end of Pipeline Road, 15-20 miles NW of Gamboa, 0-100 m, 7 Sep. 1974, *S. Mori & J. Kallunki 1731* (MO); El Llano-Cartí road, 12 Sep. 1980, *K.J. Sytsma 1062* (BM, MO); El Llano-Cartí road, 300-400 m, 9°20'N, 79°00'W, 300-400 m, 28 Aug. 1982, *C. Hamilton & H. Stockwell 1037* (MO, PMA); Cerro Jefe, near area called Los Nubes, 650 m, 9°15'N, 79°30'W, 650 m, 19 Jul. 1987, *G. MacPherson 11298* (MO, PMA); Carretera El Lano-Cartí, km 8, 9°16'42"N, 78°57'35"W, 408 m, 12 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 791* (FT, PMA, SCZ); Panamá, Parque Nacional Campana, Carretera a Chicá, 8°41'13"N, 79°55'W, 2 Feb. 2013, *M.N.S. Stapf & R.M. Baldini 940* (FT, PMA); Cerro Azul, camino hacia Cerro Jefe, 20 Jun. 2015, *Z. Mijango et al. 132* (FT, PMA); **San Blas**. In forest near waterfalls, ca. 3 miles inland Aligandí, 7 Oct. 1978, *W.G. D'Arcy & B. Hammel 12254* (MO); San Blas, El Llano-Cartí Road, 350 m, 9°19'N, 78°55W, 20 Nov. 1984, *G. de Nevers & H. Herrera 4350* (MO); **Veraguas**. Alto de Piedra, carretera Alto de Piedra-El Guabal, Km 3, 8°31'38"N, 81°07'51"W, 617 m, 18 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 843* (FT, PMA, SCZ).

PERÚ. **Huanuco**. Province Pachitea, Bosque Nacional de Iparia, 400-500 m, 15 Jan. 1969, *J. Schunke Vigo 2989* (US); **Loreto**. Maynas, Iquitos, along the Río Nanay near the Boca toma of Iquitos, 15 Feb. 1968, *D.R. Simpson & J. Schunke Vigo 658* (G, US); Río Loreto-Yacu (affluent de l'Amazone), Tierra Amarilla, 6 Feb. 1969, *C. Sastre & R. Echeverry 629* (P, US); Maynas, Río Nanay, cerca de Santa Clara, vicinity of Iquitos, 13 Jan. 1977, *J. Revilla 2136* (MO); Mayanas, Iquitos, Río Momon, vicinity Balcon, 100 m, 1 Mar 1980, *S. McDaniel & M. Rimachi Y. 23266* (MO); **San Martin**. Tarapote, 750 m, Dec. 1929, *L.O. Williams 6081* (US).

VENEZUELA. **Amazonas**. Santa Elena, Mata Cutia, 2 Nov. 1979, *N.A. Rosa & O. Cardoso 3193* (NY); Amazonas, Atabapo, extremo S de Sierra Parima, al N del Río Orinoco y al W del Río El Ejercito, 1215-1225 m, 02°19'N, 63°51'W, 8 Nov. 1982, *F. Guanchez 2101* (MO); **Anzoàtegui**. Forested slopes, Cerro La Danta, bordering tributare of Río León, NE of Bergantin, 800-1100 m, 22 Feb. 1945, *J.A. Steyermark 61115* (US); **Aragua**. Rainforest on road Maracay-Ocumara, 1 Aug. 1925, *H. Pittier 11854* (G, NY, US); Parque Nacional, 16 Mar. 1940, *A. Chase 12464* (US); Parque Nacional Henry Pittier NW of Maracay, Rancho Grande, 1150 m, 13 Nov. 1971, *G. Davidse 3022* (MO); Aragua, Autonomo Mora, Parque Nacional H. Pittier, 1050 m, 10°20'N, 67°39'W, 22 Aug. 1989, *F. Zuloaga & R. Ortiz 4510* (K, MO, US); **Barinas**. 43 km NW of the Merida intersection along road to Merida, 1000 m, 19 Nov. 1971, *G. Davidse 3193* (MO); **Bolívar**. Prope coloniam Tovar, between Coroni & Maracai, 1856-58, *A. Fendler 2495* (K); Cerro Bolívar, 1200 m, 1 Dec. 1951, *B. Maguire 32663* (NY, US); Alto Caronì, alrededores de Sta. Elena de Uairen, 25 Apr. 1946, *T. Lasser 1534* (NY, US); Sierra de Lema, cabeceras de Río Chicanàn, 80 km al SE de El Dorado, 500 m, 6°5'N, 62°W, 27 Aug. 1961, *J.A. Steyermark 89542* (NY, US); Uaipan-tepui, 5 Mar. 1967, *T. Koyama & G. Agostini 7500* (MO, NY); La Gran Sabana, 49 km W of the intersection of the main road to Santa Elena and road to Cabanayen hillside with savanna on upper slope, forest in gully, 1360 m, 3 Dec. 1973, *G. Davidse & al. 4783* (MO), (Davidse 1978); Cedeño vicinity of Panare Village of Corozal, 6 km from Maniapure toward Calcara, 300 m, 6°55'N, 66°30'W, 16 Oct. 1985, *B. Boom & M. Grillo 6418* (MO, NY); Cedeño, Serrania de Los Pijiguaos, 500-600 m, 06°33'N, 66°46'W, 29 Jan.-1 Feb. 1989, *N. Cuello 685* (MO); **Carabobo**. Autonomo Mora, 750-1000 m, 10°17'N, 68°10'W, 17 Aug. 1991, *W. Diaz 532* (MO); **Districto Federal**. Hacienda Puerto La Cruz, coastal range, 28 Aug.–10 Sep. 1918, *H. Pittier 8059* (US); Districto Federal, Colonia Tovar, 1400 m, 24 Jul. 1993, *F. Zuloaga & al. 4746* (MO); **Mérida**. Santo Domingo, 28 Sep. 1953, *L. Bernardi 993* (NY); **Miranda**. 34 km Nw of Santa Lucia along road, 200 m, 7 Nov. 1971, *G. Davidse 2910* (MO, NY, US); Mérida, on slope above dam site on Río Caparo, 31 km ESE of Santa Barbara, ca. 100-250 m, 07°41'N, 71°28'W, 9 Mar. 1980, *R. Liesner & A. Gonzalez 9256* (MO); **Portuguesa**. Bosque transicional entre La Estación y La Laguna, 15-18 km NNW de Ospino, 700-800 m, 09°25N, 69°30'W, 1 Nov. 1982, *J.A. Steyermark & al. 127004* (MO); **Sucre**. Between Zurita and El Naranjo and Agua Colorada, N of Quebrada El Naranjo and W of Río Santa Fé, 18 Aug. 1973, *J.A. Steyermark & al. 107806-A* (NY); Bermudez, Peninsula de Paria, al SE de Carupano, al NE de Maturincito, Cerro La Cerbatana, 700-750 m, 10°38'N, 63°10'30"W, 9 Jan. 2005, *W. Meier & al. 11168* (MO); **Táchira**. Uribante, Empresa Las Cuevas near La Fundacion, 900 m, 08°50'N, 71°47'W, 6 Jul. 1983, *H. van der Werff 4901* (MO); **Trujillo**. 37 km from Trujillo along road to Boconò, 13 Aug. 1964, *F.J. Breteler 4128* (MO, NY, US); **Yaracuy**. Nirgua, 5 km N of Nirgua by road, 1200 m, 10°12'N, 68°34'W, 21 Oct. 1982, G. *Davidse & al. 20890* (MO).

(14) *Lasiacis rhizophora* (E.Fourn.) Hitchc., Proc. Biol. Soc. Wash. 24: 145. 1911. (Fig. 37).

Bas.: *Panicum rhizophorum* E.Fourn., Mex. Pl. 2: 31. 1886.

Type: "*Mexico, region d'Orizaba, 10 Sep. 1866, Bourgeau 3025*" (lectotype, designated by Hitchcock 1913: 253: P! [barcode P00633945] isolectotypes, BR (photo!) [barcode BR0000006862831], C! [barcode C10017035], F (photo!) Three sheets [Acc. No. 0361411F, 0046894F], G! two sheets [barcode G00099140, barcode G00099141], K! [barcode K000309322], L! [barcode L0797263], MO! [Acc. No. MO128804], GH (photo!) [barcode GH00024122], P! Four sheets [barcode P00633943, P00633944, P00633946, P0063347], US! Fragment from P [barcode US00139935], US! [barcode US00147998]).

Nomina nuda

Panicum rhizophorum E.Fourn. ex Hemsl., Biol. Cent.-Amer. Bot. 3: 495. 1885, *nom. nud.*

Description

Perennials, semi-caespitose. *Culms* 1.0–1.5 m high, creeping, slender, rooting at the lower nodes, freely branching forming tangled colonies, erect; *internodes* 2–4 mm thick, herbaceous, puberulent, often restricted to the apex; *nodes* glabrous to puberulent. Leaf sheaths shorter than internodes, puberulent, sometime hispid, rarely glabrous, overlapping, margins usually ciliate at the apex and below, with auricular hairs prominent, 1.5–4.0 mm long; *collars* glabrous and ciliate on the margin; *ligules* 0.5–1.0 mm long, membranous, ciliate with hairs up to 3.5 mm long; *blades* 7.0–18 cm long, 1.5–4.0 cm wide, elliptic-lanceolate, adaxial surface slightly hispid, scabrid, rarely glabrous, the abaxial surface puberulent to hispid, rarely glabrous, apex acuminate, base asymmetrical. *Panicles* 10–30 cm long; *branches* ascending and spreading, scabrous to puberulent, bearing spikelets clearly clustered in pairs or small groups terminally. *Spikelets* 3.0–4.0 mm long, 2.8–3.5 mm wide; ovoid; *lower glumes* 1.5–2.0 mm long, 0.8–1.0 mm wide, 5-7-veined**;** *upper glumes* 2.7–3.0 mm long, 1.7–2.0 mm wide; *sterile florets* rarely staminate, *lemmas* 7-9-veined, *paleas* 2/3 of the fertile floret; *fertile florets* 3.0–3.8 mm long, 1.6–2.0 mm wide, black, *anthers* 1.5–1.8 mm long, whitish; *stigmas* purple; *caryopses* 2.0–2.3 mm long, 1.5–2.0 mm wide. *Chromosome number*: $2n = 36$ (Tateoka 1962); $n = 18$, $2n = 36$ (Davidse 1972, 1978).

Vernacular names

Colombia: Magdalena, "*arrocito*" *J. Cuatrecasas & R. Romero Castaneda 25383* (COL, US).

Distribution

Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Venezuela. (Fig. 38).

Distribution (bibliographic references)

Hitchcock (1913) as *L. liebmanniana* (Four.) Hitchc. and *L. rhizophora* (Four.) Hitchc.; Hitchcock (1920, 1930, 1936); Swallen (1931, 1943, 1955b); Standley (1937); Beetle (1977); Davidse (1978, 1994, 2001); Pohl (1980); D'Arcy (1987); Serna and López-Ferrari (2000); Zuloaga et al. (2003); Morales (2003); Correa et al. (2004); Hokche et al. (2008); Sutherland (2008); Acevedo-Rodríguez and Strong (2012); Villaseñor (2016); Dávila et al. (2018); Sánchez-Ken (2019); Menjivar et al. (2021).

Ecology

Lower montane wet and lower montane rain forest zones and cloudy forests, edges of forests and trails, and along streams, also in pastures and remnant montane evergreen forests. Elevation 300–1900 m.

Phenology

July through May.

Remarks

Lasiacis rhizophora is a procumbent species with culms rooting at the nodes, broad leaves, and panicles with naked branches with spikelets in small clusters. Davidse indicated it can be confused with *L. ruscifolia* but the latter never produces roots at the nodes. Contrary to what Davidse (1978) reports, I have found specimens occurring from Venezuela. *Lasiacis rhizophora* is distributed in Central America including El Salvador to northwestern South America limited to Colombia, Venezuela, and Ecuador. It is often confused in Cuba, Jamaica, and Hispaniola with *Lasiacis grisebachii*.

Selected specimens

COLOMBIA. **Cesar**. Sierra de Perijá, eastern Manaure, Hacienda Nuevo Horizonte, El Podrido, 1550–1600 m, 15–16 Nov 1959, *J. Cuatrecasas & R. Romero Castaneda 25383* (COL, US); **Valle**. La Cumbre, Cordillera Occidental, 1700–2100 m, 25–27 Sep. 1922, *E.P. Killip 11607* (NY, US).

COSTA RICA. **Alajuela**. San Miguel de San Ramon, *A.M. Brenes 20300* (NY); **Cartago**. About 4 km SW of El Tejar, 20 Aug. 1967, *R.J. Taylor 4577* (MO, NY); Along road between Navarro and El Muneco, along S side of Río Navarro, 1150 m, 9°48'N, 83°54'W, 15 Nov. 1987, *M. Grayum 8430* (MO); **Guanacaste**. Vicinity of Tilaran, 10–31 Jan. 1926, *P.C. Standley & J. Valerio 44236* (US); Los Ayotes, near Tilaran, 600–700 m, 21 Jun. 1926, *P.C. Standley & J. Valerio 45498* (US); Parque Nacional Rincon

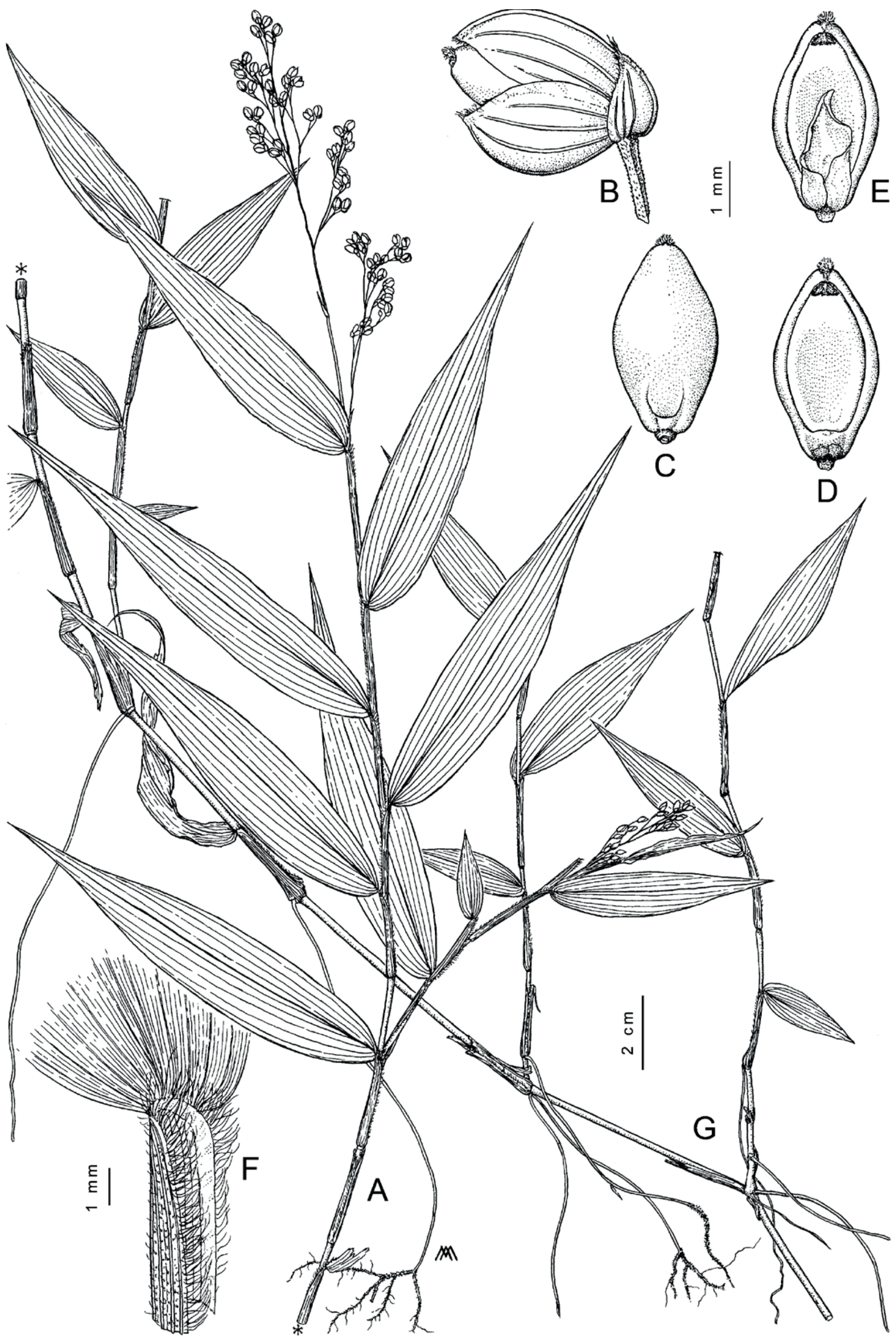

Figure 37. *Lasiacis rhizophora* (E.Fourn.) Hitchc.: **A.** Habit; **B**. Spikelet lateral view; **C**. Fertile upper floret dorsal view; **D**. Fertile upper floret ventral view without lower persistent palea; **E.** Fertile upper floret ventral floret with lower persistent palea; **F**. Ligular area; **G.** Culm at medium length rooting at the nodes (A-G. from *R.W. Pohl & G. Davidse 11481* (K)]. *A. Maury delineavit.*

Figure 38. *Lasiacis rhizophora* (E.Fourn.) Hitchc.: general geographic distribution.

de la Vieja, the SE slope of Volcán Santa Maria, above Estación Hacienda Santa Maria, 900-1200 m, 10°47'N, 85°18'W, 27-28 Jan. 1983, *G. Davidse & al. 23385* (MO); Along trail, in opening, Sendero Las Pailes, ca. 2 km W of Hacienda de Las Santa Maria, Rincon de la Vieja Nat. Park, 900-1000 m, 27 Jan. 1983, *E. Judziewicz 4295* (MO); **Puntarenas**. Monteverde, 22 Oct. 1963, *A. Jiménez 1271* (NY); Just N of the Carretera Interamericana along road to Baruca, 22 Aug. 1968, *R.W. Pohl & G. Davidse 10994* (K), **n = 18!** (Davidse 1978); Just E of Monteverde on the Pacific watershed, 10°18'N, 84°48'W, 1300-1450 m, 29 Oct.-2 Nov. 1975, *W. Burger & R. Baker 9629* (SCZ); Monteverde, 1350 m, 9 Feb. 1981, *O. Tellez 4330* (MO); Canton de Buenos Aires Ujarras, El Carmen, Sabanas de Murur Bisuk, estribaciones de Cerro Amú, 1900 m, 9°20'10"N, 83°17'40"W, 29 Sep. 1989, *G. Herrera 3601* (MO); Monteverde, pacific slope hillside 2 km below community, 1200 m, 10°17'N, 84°48'W, 2 Jan. 1990, *W. Haber 9716* (MO); Coto Brus, Parque Inter. de la Amistad, 1500-1700 m, 8°57'N, 82°50'W, 19 Nov. 1994, *S. Martén 656* (USJ); **San José**. Forets de l'Alto del Rodeo, 28 Dec. 1889, *H. Pittier 1616* (G, US, W); San José, 22-24 Oct. 1911, *A.S. Hitchcock 8502* (NY, US); Vicinity of Santa Maria de Dota, 1500-1800 m, 26 Dec. 1925-3 Jan. 1926, *P.C. Standley & J. Valerio 44071* (US); 1 mile N of San Gabriel, 29 Sep. 1968, *R.W. Pohl & G. Davidse 11179* (K, US), **n = 18!** (Davidse 1978); Along South side of canyon of the Río Birillo, near Puentes Mulas, S of San Antonio, 28 Nov. 1968, *R.W. Pohl & G. Davidse 11481* (K, US); S of Curridabat on hills, 2 Feb. 1969, *R.W. Pohl & G. Davidse 11694* (K, US), **n = 18!** (Davidse 1978); Escazú, 3 Nov. 1979, *M. Elizondo 20* (USJ).

ECUADOR. **Los Ríos**. (Pichincha?), 9 km E of Patricia Pilar, 58 km ENE of Quevedo, on Pan Am Highway to Santo Domingo de los Colorados, 300-400 m, 0°36'S, 79°18'W, 1 Jul. 1977, *H.H. Iltis & M.G. Iltis 86* (US).

EL SALVADOR. **Ahuachapán**. El Impossible Reserve, 1400 m, 89°54'W, 13°51'N, 24 Jan. 1998, *A. Monro & al. 1992* (BM, MO); Laguna Verde, 26 Jan. 1999, *R. Villacorta 2718* (BM); Laguna Verde, 31 Jan. 1999, *K. Sidwell & al. 819* (BM); **Chalatenango**. La Palma area, Caballero, 900-1500 m, 14°18'N, 89°08'W, 19 Oct. 2001, *D. Sloot 217* (MO); **Santa Ana**. Cerro Verde National Park, 2300 m, 13°29'N, 88°32'W, 23 Jan. 1998, *K. Sidwell & al. 411* (BM, BR, MO); Parque Nacional Montecristo, Cordillera de Matapan, 1900-2000 m, 14°27'N, 89°22'W, 27 Jan. 1998, *G. Davidse & al. 37158* (BM, MO); Parque Nacional Montecristo, 1800 m, 14°24'N, 89°27'W, 30 Nov. 2004, *R.A. Carballo 1142* (MO); Parque Nacional Montecristo, km 12 sobre la calle hacia Los Planes, 14°23'22"N, 89°23'15"W, 1416 m, 10 Feb. 2016, *J. Menjívar & R.M. Baldini 3481* (FT, MHES); Parque Nacional Montecristo, alrededores de la zona límite por el área de acampar 3, 14°24'29"N, 89°22'51"W, 2187 m, 12 Feb 2016, *J. Menjívar & R.M. Baldini 3654* (FT, LAGU, MHES).

GUATEMALA. **Alta Verapaz**. Coban, Sep. 1885, *H. von Tuerckheim 715* (G, K, MO, NY, P, UPS, US); Alta Verapaz, 10 km S of Coban, 1300 m, 3 Sep. 1970, *W.E. Harmon & J.D. Dwyer 4280* (MO); Along the Highway ca. 14.5 miles of Coban, 1300 m, 17 Jul. 1977, *T.B. Croat 41390* (MO); **Guatemala**. Guatemala City, 1-3 Dec. 1911, *A.S. Hitchcock 9051* (K, L, NY, US); Aldea Lo de Coy, between San Lucas and Guatemala City, 14 Nov. 1967, *A. Molina 21091* (BM, NY); 7 miles E of Guatemala City, 7 May 1970, *W.E. Harmon 2935* (NY); Vicinity of San Andrecillo, 26 Sep. 1972, *A. Molina 27554* (BM, MO, NY, US); Guatemala, El Hippodromo, 27 Nov. 1989, *L. Rodriguez 1235* (P); **Petén**. Laguna Macanché, Flores, 181 m, 16°58'25"N, 89°37'23"W, 23 Oct. 2008, *J. Morales 4947* (MO); **Quezaltenango**. Along old road between Finca Pirineos and Patzulín, 9 Feb. 1941, *P.C. Standley 86730* (US), *86758* (K); Along the Highway Cito N of junction CA2, toward Quezaltenango, in watershed reserve INDE, Santa Maria, km 199, loose gray soil, steep slopes W of Highway, 14°45'N, 91°32'W, 22 Jan. 1987, *T.B. Croat & D.P. Hannon 63145* (MO); **Sacatepéquez**. Nascimento del Cangrejal, Cuestas de Las Cañs, 3 Feb. 1949, *A. Molina 15446* (US); **San Marcos**. Between San Rafael Pie de la Cuesta and Palo Gordo, Sierra Madre Mts., 10-18 Dec. 1963, *L.O. Williams & al. 26039* (NY, US, W); **Santa Rosa**. Chupadero, Oct. 1892, *E.T. Heyde & Lux 3915* (BM, G, K, US).

HONDURAS. **El Paraíso**. Monserrat Mountain, 12 Aug. 1971, *A. Molina 26149* (BM, NY, US); El Paraíso, Monserrat Mountain, 6 Aug. 1972, *A. Molina 27483* (BM, US); **Lempira**. Near Gracias, Montaña de Celaque, 20 Sep. 1991, *M. Chorley 342 pro parte* (MO); **Morazán**. About 6 km W of Siguatepeque, 8 Aug. 1936, *T.G. Yuncker 6388* (NY); Caminos Tatumbla, Labranza y Quebrada El Granadillo, sobre la Mt. Uyuca, 4 Nov. 1948, *A. Molina 1433* (US); Cerro de Uyuca, trail between Las Flores and La Labranza, 22 Aug. 1949, *P.C. Standley 23109 a* (NY, US); Mt. Uyuca, 20 Sep. 1949, *L.O. Williams 16851* (BM); Mt. Uyuca entre Quebrada Granadillo Y Labrança, 27 Jul. 1950, *A. Molina 2766* (BM, US); Mt. Uyuca, 19 Oct. 1951, *J.R. Swallen 10903* (MO, US); Morazán, Río Rancho Quemado, SE of Tegucigalpa, 9 Nov. 1966, *A. Molina 18651* (BM, NY, US, W); Between La Vuelta del Zope and San Juan del Rancho, 20 Sep. 1970, *A. Molina & al. 25824* (MO, NY, US); El Zamorano, Escuela Agricola Panamericana, Cerro Uyuca, 1600 m, 17 Nov. 1970, *G. Davidse & R.W. Pohl 12489* (MO), **n = 18!** (Davidse 1978); Quebrada Hierba Buena, Valle de Angeles, 15 km NE de Tegucigalpa, 24 Sep. 1983, *C. Calderón 83* (K, MO); Los Limones, 21 km N of Tegucigalpa, 22 Oct. 1988, *Murillo 134* (BM); **Santa Barbara**. Vicinity of Sta. Barbara, 22 Aug. 1968, *A. Molina 22013* (NY).

MEXICO. **Chiapas**. Between Escuipulas and Cañada Honda, 5 Nov. 1945, *E. Hernandez Xolocotzi 309* (US); Sierra Madre, 1300 m, 3 Nov. 1960, *T. Tateoka 1030* (US); Trinitaria, Lago de Monte Bello, 25 miles E of La Trinitaria, 17 Aug. 1966, *D.E. Breedlove 14999* (US); La Trinitaria, along the Comitan River at its sumidero, Lagos de Montebello, 42 km NE of La Trinitaria, 1300 m, 23 Oct. 1971, *D.E. Breedlove 21101* (MO); Cintalapa, 16 km NW of Rizo de Oro along logging road to Colonia Figaroa, 1600 m, 3 Nov. 1971, *D.E. Breedlove 21703* (MO); Ocosingo, 6-8 km N of Ocosingo along road to Bachajon, 24 Sep. 1972, *D.E. Breedlove 27923* (MO, NY); Tenejapa, Pocolum, 15 Sep. 1982, *A.M. Ton 4609* (US); Tuxla-Gutierrez, El Sumidero (Coyota), 18 Oct. 1974, *R. Bavazzano s.n.* (FT); San Fernando, 4-6 km W of Mirador Los Chiapas in Parque Nacional del Sumidero, 14 Nov. 1984, *G. Davidse & al. 29728* (K); **Guerrero**. Galeana, 15 Oct. 1937, *G.B. Hinton 10809* (NY), 16 Oct. 1937, *10809a* (K); Vallecitos, Montes de Oca, 10 Sep. 1937, *G.B. Hinton 11381* (MO); Galeana, Carrizo-Molino, 14 Oct. 1939, *G.B. Hinton 14633* (NY, US, W); **Oaxaca**. Putla, a 14 km al N de Putla de Guerrero, 28 Oct. 1980, *O. Tellez 3940* (MO); 15 km E of San Gabriel Mixepec, 18 Sep. 1973, *S.R. Hill 1681* (NY); Pluma Hidalgo, Pochutla, Cerro Espino, al E de la finca cafetalera Monte Cristo, 1250 m, 15°52'N, 96°24'W, 2 Oct 1988, *A. Campos V. 2503* (MO); **San Luis de Potosí**. Salina, Montecristo, Jan. 1938, *E. Matuda 1939* (K, US); **Veracruz**. Orizaba, Aug. 1854, *M. Botteri 150, 151* (BM, US, P); Córdoba, 27 Aug. 1910, *A.S. Hitchcock 413* (BM, BR, C, G, K, L, MO, NY, P, US, W).

NICARAGUA. **Estelí**. Cerro Quiabú, 8 Km NO de la ciudad de Estelí, 1500-1600 m, 19 Oct. 1979, *A. Grijalva & M. Araquistain 623* (PMA); Cerro Quiabú (Cerro Las Brisas), 24 Nov. 1979, *W.D. Stevens & al. 16212* (BM); Condega, Comunidad Venecia, del albergue Cantagallo 250 m al Norte, 600-800 m, 13°24'60"N, 86°14'25"W, 8 Jan. 2008, *C.A. Padilla Gomez 132* (MO); **Granada**. Summit of Mt. Mombacho, near Grenada, 18 Dec. 1940–9 Feb. 1941, *V. Grant 821* (US); W del Volcán Mombacho al tope del camino de Finca El Progreso, 11°50'N, 85°59'W, 1250 m, 22 Nov. 1981, *J.C. Sandino 1584* (MO); **Jinotega**. 142 km from Managua to La Fundadora, 7 Dec. 1958, *J.G. Hawkes 2192* (C, G, K); Carretera Matagalpa-Jinotega, 1300 m, 13°03'45"N, 85°59'W, 2 Nov. 1983, *S. Vega & B. Quezada 19* (MO); **Madriz**. Carretera a Cusmapa, a 17 km de Somoto El Silencio, 1200-1300 m, 13°20'N, 86°37'W, 18 Sep. 1982, *P.P. Moreno 17603* (MO); **Matagalpa**. La Harmonia and lower S slope of Cerro El Picacho, 1200-1350 m, 13°00'N, 85°55'W, 15 Sep. 1984, *W.D. Stevens 23104* (MO).

PANAMA. **Bocas del Toro**. Campamento de Lucho, 09°05.052N 082°44.733W, 1850 m, bosque nuboso, muy humedo, 17 Mar. 2004, *E. Alfaro & A.K. Monro 5597* (PMA); **Chiriquí**. E slope of Volcán de Chiriquí (Barú), WNW of Boquete, 19 Nov. 1975, *G. Davidse & D'Arcy 10158* (K, MO, US), **n = 18!** (Davidse 1978); Cerro Colorado mining road 15.6 miles above bridge over Río San Felix, 1330 m, 21 Nov. 1979, *T. Antonio 2568* (MO); Road between Finca Lerida and San Ramon, along Quebrada El Velo, 8 Mar 1989, *P.M. Peterson & C.R. Annable 7369* (MO); Orillas de la carretera Gualoca-Fortuna, a 500 m despues de los Planos de Hornitos, 8°12'13"N, 82°12'41"W, 1024 m, 20 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 855, 856* (FT, PMA, SCZ); Carretera a Aguacatal, SW del Volcán Barù, 8°47'36"N, 82°34'54"W, 23 Jan. 2012, *M.N.S. Stapf, & R.M. Baldini 873, 876, 877* (FT, PMA, SCZ); Carretera Volcán-Río Sereno, puente sobre al Río Chiriquí Viejo, 848'27"N, 8240'W, 1338 m, 23 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 896* (FT, PMA, SCZ); Carretera de Alto Boquete-El Salto, 846'49"N, 82°27'52"W, 1520 m, 24 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 903, 905* (FT, PMA, SCZ); Gualaca, Reserva Forestal Fortuna, Sendero Hornitos, 8°40'53"N, 82°13'05"W, 1346 m, 5 Nov. 2013, *O.O. Ortiz & al. 1757* (FT, PMA); **Los Santos**. Guararé, a 300 mts. de la carretera Nacional, 23 Jul. 1974, *F.M. Saavedra 13* (PMA); **Veraguas**. El Cuchillo near Cerro Tute, up from Santa Fé, 1300 m, 8°32'N, 81°07'W, 8-9 Sep. 1982, *C. Hamilton & al. 1244* (MO).

VENEZUELA. **Lara**. Jimenez, Parque Nacional Yacambú, 3km E of Park headquarters, Quebrada El Blanco, 09°43'N, 69°34'W, 1300-1400 m, 24 Oct. 1982, *G. Davidse & A.C. González 21089* (MO); **Portuguesa**. Selva bordeando una laguna natural en la fila de la cumbre, 17.8 km de La Estación, 30 km al Norte de Ospino, 1 Nov. 1982, 1170 m, *J.A Steyermark & al. 126948* (MO).

(15) *Lasiacis rugelii* (Griseb.) Hitchc., Bot. Gaz. (Crawfordsville) 51: 302. 1911. (Fig. 39).

Bas.: *Panicum rugelii* Griseb., Cat. Pl. Cub. 233. 1866.

Type: "*Cuba, in montibus Mantanazas, scandens in fruticibus, 1849, Rugel 188*". Lectotype, designated by Hitchcock 1909: GOET! (photo) [Acc. No. GOET009532]; isolectotypes, BM! Two sheets [barcode BM000938723, BM000938724], GH! (photo) [barcode GH00023863], GOET (photo!) [Acc. No. GOET009533], L! [barcode L0044661], NY! [barcode NY00071073], US! Fragment from GOET [barcode US00139946]).

(=) *Lasiacis papillosa* Swallen, Publ. Carnegie Inst. Wash. 436: 349. 1934.

Type: "*Mexico, Yucatán, Peto, erect in bush, 26-27 July 1932, J.R. Swallen 2707* (holotype: US! [barcode US00134117]; isotype K! [barcode K000309324], MO! [Acc. No. MO128802]).

(=) *Lasiacis lancifolia* Swallen, Publ. Carnegie Inst. Wash. 436: 349. 1934.

Type: "*Mexico, Yucatán, Muna, along trail in hills, culm erect, 22-23 July 1932, J.R. Swallen 2664*" (holotype: US! [barcode US00134107]; isotypes, GH (photo!) [barcode GH00023859], MICH (photo!) [Acc. No. MICH1108700], K! [barcode K000309323], US! Five sheets [barcode US00134103, US00134104, US00134105, US001334106, US00134103]).

Description

Perennials, caespitose. *Culms* 0.5-3(-4.0) m long, erect, clambering and climbing, prostrate, upper part usually strongly zigzag, older culms branched; *internodes* 2-5 mm thick, hollow, mostly lignified, papillose-puberulent with appressed hairs, rarely glabrous or shortly pubescent; *nodes* usually glabrous. *Leaf sheaths* spreading puberulent, sometimes the lower margins ciliate, auricles with hairs 2 mm long; *collars* puberulent; *ligules* 0.2-0.3(-0.4) mm long, inconspicuous, glabrous, or ciliolate with hairs 0.5 mm long; *blades* 2.5-5.5(-8.0) cm long, 0.5-1.5(-2.0) cm wide, lanceolate, or oblong-lanceolate, hispidulous or puberulent on both surfaces, base asymmetrical, apex acute to acuminate, margins scabrid. *Panicles* 4-12 cm long, few-flowered; *branches* bearing few spikelets, proximal branches and most branchlets reflexed; *pedicels* finely pubescent. *Spikelets* 4.5-5.0(-7.0) mm long, 2.0-2-4 mm wide; obovate; *lower glumes* (1.8) 2-2.5 mm long, 1.3-1.5 mm wide, 7-9-veined; *upper glumes* 3.5-4.8 mm long, 1.8-2.0 mm wide, 9-11-veined; *sterile florets* without flowers, *lemmas* 9-11-veined, *paleas* ¾ to subequal to the length of the fertile floret; *fertile florets* 4.0-5.0 mm long, 2.0-2.5 mm wide; *anthers* 2 mm long, whitish; *stigmas* white; *caryopsis* 2.4-2.7 mm long, 2.0 mm wide. *Chromosome number*: unknown.

Iconographs

Lámina 154 (Catasús Guerra 2012b).

Vernacular names

Cuba: "*pitilla*" (Acevedo-Rodríguez and Strong 2012; Roig 1963; Catasús Guerra 2012a).

Distribution

Belize, Cuba, Dominican Republic, Guatemala, Haiti, Honduras, Mexico. (Fig. 40).

Distribution (bibliographic references)

Hitchcock (1909) as *Panicum rugelii* Griseb.; Hitchcock (1911, 1920); Hitchcock and Chase (1917); Swallen (1934) as *L. lancifolia* & *L. papillosa*; Swallen (1936, 1955b) as *L. papillosa* Swallen; Beetle (1977); Davidse (1978, 1994); Serna and López-Ferrari (2000); Zuloaga et al. (2003); Morales (2003); Sutherland (2008); Acevedo-Rodríguez and Strong (2012); Catasús-Guerra (2012a); Sylvester (2016); Villaseñor (2016); Dávila et al. (2018); Sánchez-Ken (2019).

Ecology

Edges of forests, trails, in thickets; frequent in secondary forests and in pine forests (Cuba). Sea level to 800 m.

Phenology

Throughout the year, more frequent June through March.

Remarks

Lasiacis rugelii, as pointed out above, is related to *L. pohlii*. It has erected culms, rarely prostrate, and forms a zigzag stem pattern resembling *L. divaricata* but differing from the latter in having shorter and wider leaf blades and puberulent culms and leaves. Davidse (1978) gives a detailed summary of the synonyms of this species, such as *L. papillosa* Swallen, and *L. lancifolia* Swallen, both described from Mexico, while Beetle (1977) and Ulloa Ulloa et al. (2025), erroneously, consider them as valid species. *Lasiacis rugelii* is typically a northern Central American species extending to the Caribbean

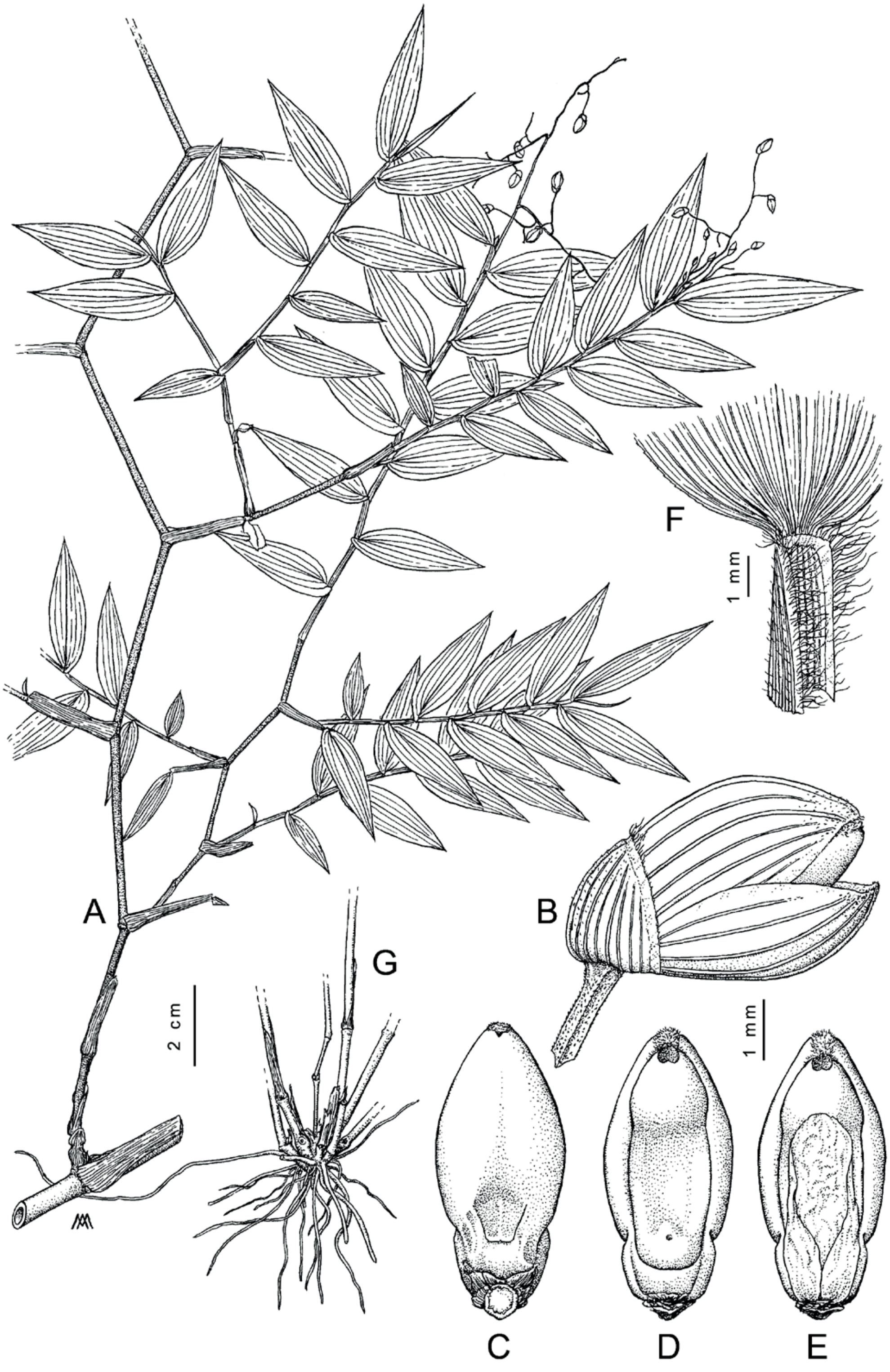

Figure 39. *Lasiacis rugelii* (Griseb.) Hitchc.: **A.** Habit. **B**. Spikelet lateral view; **C**. Fertile upper floret dorsal view; **D**. Fertile upper floret ventral view without lower persistent palea; **E**. Fertile upper floret ventral view with lower persistent palea; **F**. Ligular area [A-F. from *P.H. Gentle 1218* (K)]; **G**. Base of the culm [G. from *E.L. Ekman 12845* (K)]. *A. Maury delineavit*.

Figure 40. *Lasiacis rugelii* (Griseb.) Hitchc.: general geographic distribution.

whereas *L. pohlii* is definitely more common in Costa Rica and Panama (see also Davidse 1978).

Selected specimens

BELIZE. **Belize**. 21 Jun. 1973, *T.B. Croat 24770* (K, L, MO, NY, US); **Cayo**. Mountain Pine Ridge, Jul.-Aug. 1936, *C.L. Lundell 6840* (BM, C, MO, NY); Hummingbird Highway, 8 Dec. 1955, *P.H. Gentle 8974* (BM, G, NY, US); El Belize-Cayo Road, 26 Mar. 1958, *P.H. Gentle 9691* (G, MO, NY, US); Cayo-Belize road, 17°17'N, 88°39'W, 28 Nov. 1968, *R.R. Innes 49* (K); Millionario, 12 Dec. 1968, *G.R. Proctor 29865* (BM); Mountain Pine Ridge, Blancaneaux Lodge, 17 Aug. 1970, *J.R. Wiley 400E* (MO); Macal (Macaw) River, Guacamallo Bridge, 29 Jan. 1974, *J.D. Dwyer & R. Liesner 12284* (MO); S of Guacamallo Bridge, 10 May 1981, *C. Whitefoord 2826* (BM, K); Near Terra Nova Forest Reserve, ca. 21 km N of Black Man Eddy Village and Belize River, 100 m, 17°21'N, 88°55'W, 6 Jul. 1995, *D.E. Atha & al. 1013* (MO, NY); **Maskall**. 16 Apr. 1934, *P.H. Gentle 1218* (K, MO, NY, US); **Orange Walk**. Honey Camp, 1928, *C.L. Lundell 91* (K); Orange, Honey Camp, Oct. 1929, *C.L. Lundell 550* (BM, K, MO, NY, UPS, US); Orange Walk District: Blue Creek-Gallon Jug Road, 1 Nov. 1989, *P.W. Alcorn 786* (FTG); **Stann Creek**. Commerci Bight Pine Ridge, 12 Nov. 1953, *P.H. Gentle 8094* (NY); **Toledo**. Near Macaca, 13 Dec. 1949, *P.H. Gentle s.n.* (BM, G); Lower slopes of Richardson Peak, Maya Mountains, directly N of the junction of R. Creek and Blanden Branch, 300-620 m, 16°33'N, 88°46'30"W, 4, 6, 8, Mar. 1987, *G. Davidse & A.E. Brant 31968* (MO); Las Sierritas, 20 km W of Big Creek Settlement, S slopes of the western most range of the Las Sierritas hills, 40-80 m, 16°31'30"N, 88°37'30"W, 5 Dec. 1997, *T. Hawkins 1669* (MO).

CUBA. 1860-1864, *C. Wright 3465* (G, MA, NY, P, US, W); **Habana**. Habana, San Antonio, 20 Mar. 1906, *A.S. Hitchcock 176* (US); Habana, Marianao, 23 Oct. 1921, *E.L. Ekman "Amer. Gr. Nat. Herb. no. 795"* (BM, C, G, K, L, NY, P, US, W); Lomas de Camoa, 22 Nov. 1921, *E.L. Ekman 13516* (US); Habana, Loma della Pita, San Miguel de Casanova, 6 Dec. 1923, *Bro. León 12462* (US); **Mantanzas**. Vicinity of Mantanzas, Playa, 12 Mar. 1903, *N.L. Britton, & al. 106* (NY); NW of Pan de Mantanzas, S of Canasì, 31 May 1923, *E.L. Ekman 16489* (US); **Nueva Gerona**. Isle de Pines, Coe's Camp, Ensenada de Siguanea, 25 Feb. 1916, *N.L. Britton & P. Wilson 14860* (NY, US); Isles of Pines, Cayo del Res, on the southern side of Cienaga Panier, 2 Dec. 1920, *E.L. Ekman 12446* (US); **Oriente**. Guantanamo, Norte Libanon, 700 m, 25

Dec. 1919, *E.L. Ekman 10306* (US); Sierra de Nipe, 24 Nov. 1922, *E.L. Ekman 15242* (G, US); Peninsula de Cabo Cruz, S of Viquero between Río Nuevo and the coast, 16 Jan. 1923, *E.L. Ekman 16157* (NY, US); **Pinar del Río**. Mts. Near Taco Taco, 28 Oct. 1904, *C.F. Baker 3790* (NY, W); Pinar del Río, Sierra Anafe, 20 Dec. 1911, *P. Wilson 11449* (NY, US); San Cristobal, Loma del pimento, 29 Nov. 1920, *E.L. Ekman 11526* (G); San Cristobal, 2 Jun. 1921, *E.L. Ekman 12845* (G, K).

DOMINICAN REPUBLIC. Cordillera Septentrional, Prov. Puerto Plata, Sosña, coastal thickets at La Goleta, 26 Mar. 1930, *E.L. Ekman 14531* (C, K, NY, US); Cordillera Septentrional, Prov. Monte Cristi, Sabana Cruz (Puerto Rico), en uma loma al norte de la carretera, suelo pedregoso, zona seca con vegetación original poco alterada, abundante *Coccoloba* y *Diospyros*, 19°49'N, 71°22'W, 5 Dec. 1985, *R. García & J. Pimentel 840* (NY).

GUATEMALA. **Alta Verapaz**. Along the Río Polochic below Tamahù, 975 m, 10 Apr. 1941, *P.C. Standley 91779* (US); Finca Argentina above Papalha, 15 miles W of Teleman on road from Tucuru to El Estor, 550-650 m, 19 Jul. 1977, *T.B. Croat 41538* (MO); **Izabal**. WNW of (above) El Estor, along margin of open pit nickel mine, 410 m, 30 Aug. 1988, *W.D. Stevens & E. Martinez S. 25220* (MO); El Estor, La Llorona, 300 m, 23 Aug. 1998, *M. Véliz 7024* (MO); **Petén**. Tikal National Park, in secondary growth bordering airfield, 13 Feb. 1959, *C.L. Lundell 15531* (US), *15713* (G), 2 Jul. 1959, *C.L. Lundell 16106* (C, G); Tikal National Park, in secondary growth bordering airfield, 23 Jun. 1960, *E. Contreras 1151* (G, US); Dos Lagunas, 22 Dec. 1960, *E. Contreras 1738* (US); Santo Toribio, 27 Jul. 1961, *E. Contreras 2692* (US); Tikal National park, Tikal, on Temple IV, 17 Jan. 1962, *C.L. Lundell 17145* (US); Santa Ana, 20 km E de Santa Elena, 13 Nov. 1965, *A. Molina 15680* (US); 6 km SE de la aldea Uaxactum, 25 May 1973, *R.T. Ortiz 2648* (US); 2 miles south of entrance of Tikal National Park, 500 ft., 19 Jun. 1973, *T.B. Croat 24709* (F); Lago Petén, Itzá, 260 m, 17°07'N, 89°53'W, 20 Aug. 1993, *B. Wallnöfer & al. 5981* (K, MO, W); Parque Nacional Laguna del Tigre, 27 Jun. 1999, *M. Peña-Chocarro & al. 554* (BM, MO).

HAITI. **Nord Ouest**. Nord of Montry, Ile la Tortue, in limestone rock, 7 Jun. 1925, *E.L. Ekman 4254* (G, MO, K).

HONDURAS. Along Yaragua Creek, 1 mile W of Copan Ruinas, 500 m, 29 Aug. 1975, *A. Molina R. 30846* (MO); Río Frio at edge of tall bunch-grass pine savanna, 1450', sandy soil, 16°34'N, 88°54'W, 13 Dec. 1959, *D.R. Hunt 266* (BM); Islas da Bahía, Guanaj, 9 Mar. 1988, *Vásquez 107* (BM).

MEXICO. **Campeche**. Campeche, 8 Nov. 1931, *C.L. Lundell 918* (BM, NY, US); Champoton, a 38 km al S del km 98 de la carretera Escarsega a Chetumal, sobre el camino a las ruinas de Calakmul, 200 m, 4 Feb. 1983, *E. Martinez S. 2960* (MO); Camino a Palizada entre Santa Adelaida a Santa Elena, 5 m, 28 Jan. 1986, *C. Chan 6049* (F); Calakmul, 9 km S of La Nueva Vida, on road Xpujil-Campeche, 22 Nov. 1997, *E.M. Lira 368* (BM); Calakmul, 10 km SE from Dos Naciones, road to El Civalito, 4 Dec. 1998, *E. Martínez 31463* (BM); Calakmul, a 3 km al E de 16 de Septiembre, camino a Santa Rosa, 299 m, 18°05'N, 89°14'W, 5 Dec. 1998, *E. Martinez 31503* (MO); Calakmul, a 11 km al S de San Antonio Soda, camino a Los Angeles, 200 m, 18°19'31"N, 89°10'30"W, 21 Feb. 2002, *E. Martínez 35000* (MO); Calkmul, a 3 km al NE de Conchuas, camino a Nadzcaan, 195 m, 18°33'21"N, 89°53'49"W, 23 Oct. 2002, *D. Alvarez 2211* (MO); **Quintana Roo**. Chichancanab (Laguna Chan-kabnab), 28-29 Jul. 1932, *J.R. Swallen 2761* (K, US); San Miguel, Cozumel Island, 6-8 Aug. 1932, *J.R. Swallen 2879, 2887, 2902* (US); Quintana Roo, Tancah, 4 Aug. 1932, *J.R. Swallen 2824* (US); Lake Tabasco, Balancan, 29 Oct. 1975, *A. Novelo & al. 30* (K, MO); Road between Mérida and Chunhuhub, 14 Oct. 1980, *O. Téllez 3669* (BM); Sobre el Km 4 de la Brecha, camino del Norte, 6 Nov. 1980, *E. Cabrera 99* (NY); Vallarta, 2 km S of Puerto Morelos, 13 Feb. 1981, *E. Cabrera 1129* (BM); 20-22 km W of Puertos Morelos, 5 May 1982, *G. Davidse & al. 20094* (BM, MO); 8 km N of Uníon, 7 May 1982, *G. Davidse & al. 20142* (BM, MO); Near San José de la Montaña, on road to Thomás Garrido, W of Chetumal, 9 May 1982, *G. Davidse & al. 20261* (BM, MO); Othon P. Blanco, a 12 km al NO del poblado Río Verde, camino al Rancho El Vergel, 87 m, 19°04'N, 89°06'W, 30 Apr. 2004, *D. Alvarez 8769* (MO); **San Luis de Potosí**. Rascon, Río de Los Gallures, Aug. 1911, *C.A. Purpus 5438* (BM, L, MO, NY, US); **Tabasco**. Quintana Roo, S of F. Carrello Puerto, 8 Aug. 1980, *O. Téllez 3021* (BM); **Veracruz**. Vicinity of Río Tonto, Ejido de Almilinga, 6 km W of Campo Experimental de Hule El Palmar, Zongolica, 30 Jul. 1943, *J.V. Santos 2269* (NY); Panuco, Cerro de Topila, ladera de Santa Fé, 160 m, 22°06'N, 98°00'W, 26 Nov. 1985, *C. Gutierrez B. 1614* (MO); **Yucatán**. Izamal, s.d., *G.F. Gaumer 1032* (C, G, P, NY); Lak Chichankanab, Apr. 1917, *G.F. Gaumer & al. 23685* (G, NY, US); Chichen Itzá, 7-13 Jul. 1932, *J.R. Swallen 2445* (K, US), *2464* (US); Tizimin, 14-16 Jul. 1932, *J.R. Swallen 2518* (US); Peto, 26-27 Jul. 1932, *J.R. Swallen 2677* (K, US), *2713* (K, US), *2716* (K), *J.R. Swallen 2696, 2697, 2698, 2712, 2713* (MO, US); Muna, 22-23 Jul. 1932, *J.R. Swallen 2665* (US); 3 km W de Koncal, 16 Oct. 1993, *L. Rico & G. Campos 1177c* (K, US).

(16) *Lasiacis ruscifolia* (Kunth) Hitchc., Proc. Biol. Soc. Wash. 24: 145. 1911. (Fig. 41).

Bas.: *Panicum ruscifolium* Kunth, Nov. Gen. Sp. Pl. 1: 101. 1816.

Type: "*In aprici set aridis regni Mexicani, ad mont. Jorullo, alt. 490 hexap*" (**lectotype, designated here**: P! [barcode P00128869] isolectoypes BM! [barcode BM000938728], P! Three sheets [barcode P00128868, P00128870, P00128871]).

[*Lasiacis ruscifolia* (Kunth) Hitchc. & Chase, Contr. U.S. Natl. Herb. 18(7): 339. 1917, *isonym*.].

(=) *Panicum compactum* Swartz, Adnot. Bot. 14. 1829, non Kit. (1814).

Type: "*Jamaica, Swartz s.n.*" (holotype: S [Acc. No. S06-633]; isotype BM ! [barcode BM000938725]).

(≡) *Lasiacis compacta* (Swartz) Hitchc., Proc. Biol. Soc. Wash. 24: 145. 1911.

(=) *Panicum liebmannianum* E.Fourn., Mex. Pl. 2: 33. 1886.

Type: "*Mexico, Consoquitla, Aug. 1841, Liebmann 299*" (**lectotype, designated here**: C! [barcode C10017037];

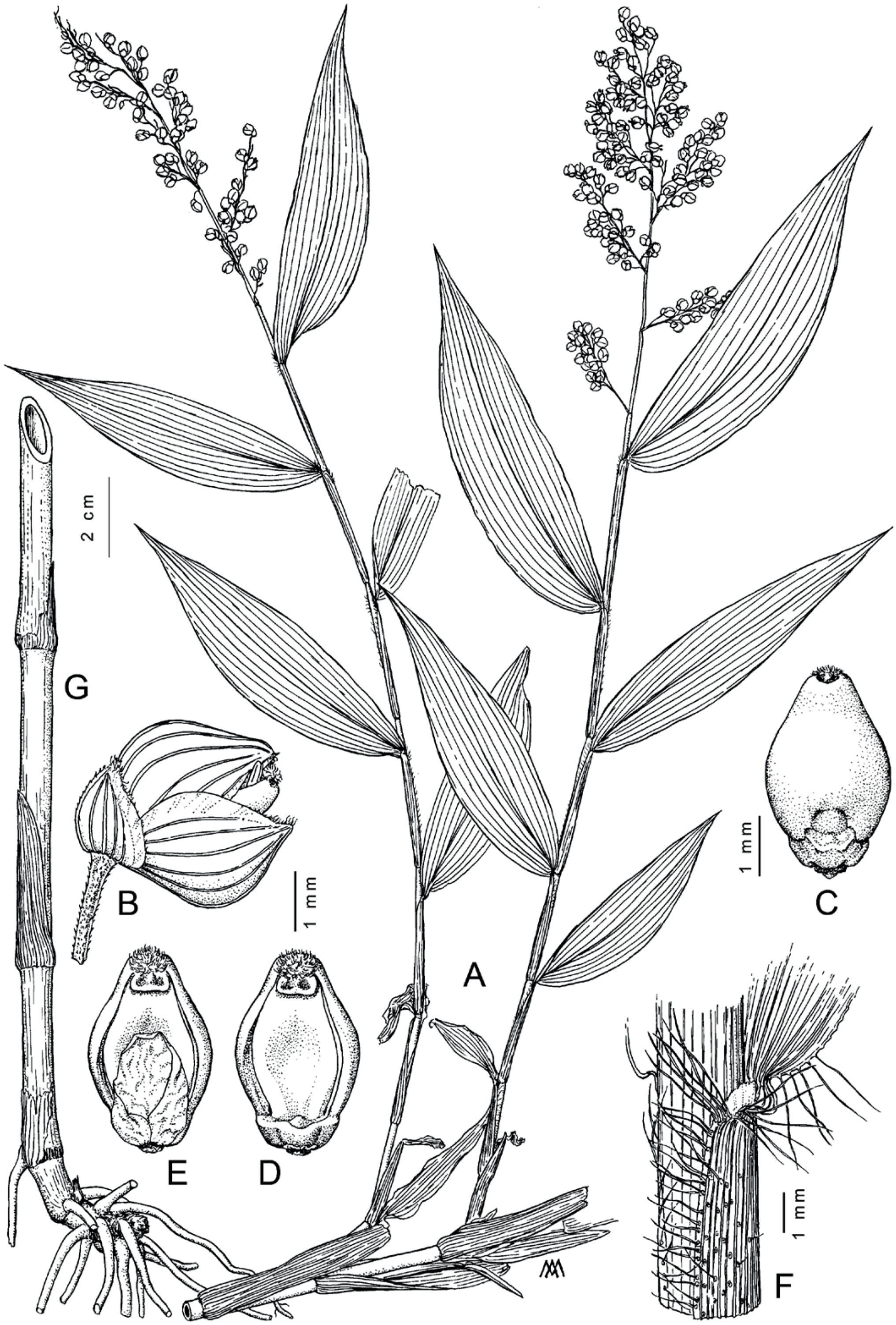

Figure 41. *Lasiacis ruscifolia* (Kunth in F.H.W. von Humboldt, A.J.Bonpland & C.S.Kunth) Hitchc.: **A.** Habit with terminal fertile branches; **B**. Spikelet lateral view; **C**. Fertile upper floret dorsal view; **D**. Fertile upper floret ventral view without lower persistent palea; **E**. Fertile upper floret ventral view with lower persistent palea; **F**. Ligular area **G.** Culm towards the base with persistent leaf sheaths and prop roots [A-G. from *V. Nilsson & R. Manfredi 536* (K)]. *A. Maury delineavit.*

isolectotypes: C! [barcode C10017036], US! Fragment from C [barcode US00148246]).

(≡) *Lasiacis liebmanniana* (E.Fourn.) Hitchc., Proc. Biol. Soc. Wash. 24: 145. 1911.

(=) *Panicum liebmannianum* Fourn, var. *depauperatum* E.Fourn., Mex. Pl. 2: 33. 1886.

Type: "*Mexico, inter Guatulco et S. Miguel del Puerto, Oct. 1842, Liebmann 280*" (lectotype, designated by Davidse 1978: C! [barcode C10017040]).

(=) *Panicum ruscifolium* Kunth var. *amblyoides* E.Fourn., Mexic. Pl. 2: 34. 1886.

Type: "*Mexique, San Louis de Potosí, Virlet 1299*" (**lectotype designated here**: P! [barcode P00642279]; syntypes: "*Mexico, Consoquilta Mar 1842, Liebmann 292*". C (n.v.); US! Fragment from C [barcode US00139950]; *Cuernavaca, 14 Janv. 1865, Bilimek 449* P! [P00642280, P00642281, P02256074]).

(=) *Lasiacis globosa* Hitchc., Contr. U.S. Natl. Herb. 17: 251. 1913.

Type: "*Mexico, Acapulco and vicinity, October 1894-March 1895, Dr. Edward Palmer 114*" (holotype: US! [barcode US00134102]; isotypes GH (photo!) [barcode GH00023858], MO! [Acc. No. MO703510], US! [barcode US00134101]).

(=) *Lasiacis glabra* Swallen, Ceiba 4: 287. 1955.

Type: "*Honduras, El Paradiso, road to Danlí, moist shady banks near Río San Francisco, 1 November 1951, J.R. Swallen 11193*" (holotype: US! Three sheets [barcode US00134098, US00134099, US00134100]; isotypes G! [barcode G00099139], NY! [barcode NY00381280], P! [barcode P00633951]).

Nomina nuda

Panicum ruscifolium Kunth var. *amblyoides* E.Fourn. subvar. *glabra* E.Fourn., Mex. Pl. 2: 34. 1886. *nom. nud*.

Panicum ruscifolium Kunth var. *amblyoides* E.Fourn. subvar. *pilosa* E.Fourn., Mex. Pl. 2: 34. 1886. *nom. nud*.

Description

Perennials caespitose. *Culms* 1-8 m long, robust, erect at the base, arching, leaning on vegetation; *internodes* 5-14 mm thick, hollow, lignified, glabrous to puberulent, sometimes pubescent; *nodes* glabrous. *Leaf sheaths* usually hispid, with hairs up to 3.5(-3.8) mm long, sometimes puberulent to glabrous, overlapping margins ciliate with hairs 0.5-2.3 mm long, auricles hairy with hairs up to 3 mm long; *collars* puberulent or glabrous, rarely pubescent; *ligules* 0.3-1.0 mm long, semi-inconspicuous, glabrous or ciliate with small hairs 0.5-0.8 mm long; *blades* 4.0-15 cm long. 1.5-6.0 cm wide, ovate to ovate-lanceolate, glabrous, puberulent to villous, base asymmetrical, enrolling the culm, margins scabrid, apex acute to acuminate. *Panicles* 5-25 cm long, dense to open and widely spreading at maturity, scabrous. *Spikelets* 2.5-4.0 mm long, 2.3-3.8 mm wide, ovate-globose; *lower glumes* 1.4-2.0 mm long, 0.8-1.5 mm wide, 9-13-veined; *upper glumes* 3.0-4.0 mm long, 1.8-2.5 mm wide, 11-13-veined; *sterile florets* without flowers, *lemmas* 11-14-veined, base of the fertile lemma with a clear protecting shelf, *paleas* 2/3 the length of the fertile floret, deeply concave; *fertile florets* 2.7-4.0 mm long, 2.0-3.0 mm wide, ovoid, darkish to black, *anthers* 1.5-2.2 mm long, whitish, *stigmas* white; *caryopses* 2.0-2.5 mm long, 1.5-2.0 mm wide. *Chromosome number*: $2n = 36$ (Tateoka (1962); $2n = 36$ (Reeder 1967); $n = 18$, $2n = 36$ (Davidse 1972, 1978).

Iconographs

Fig. 87 A-B (Renvoize 1998); Davidse (2003: 391); Lámina 158 (Catasús Guerra 2012b).

Vernacular names

El Salvador: "*carrizo*", "*carrizo montés*", "*cebadita*", "*arrocillo*" ("*padilla*") (Standley and Calderón 1925); **Mexico**: "*carricillo*", "*carrillo*", "*kcua*", "*mehesit*", "*otatillo*", "*pacab*", "*sit*", "*thimaloon pakab*", "*tsahib kw'a*'", "*tsakam pakamb*", "*tsay'kw's*", "*tseey kw'a pulik*", "*tsooy kw'a*", "*tzaicuo*" (Quattrocchi 2006), "*zit*", (Steggerda 1943), "*mehen zit*" (Standley 1930; Roys 1931), "*carrizito*" (Rebman et al. 2016); **Nicaragua**: Managua, "*caricillo*" (*Bro. A. Garnier 1241* (US); **Panama**: "*carrizo*" (Swallen 1943), "*lágrimas de le Virgem*", *S. Knapp 1241* (MO); **Puerto Rico**: "*carrucillo*", "*pito de alfombra*" (Acevedo-Rodríguez and Strong 2012).

Ethnobotanical and economic uses

"*Stems are used as whistles by Maya boys, water sucking stick, and for carpet weaving*" (Staggerda 1943); "*construction and technical uses, and in the thatching of hurts*" (Lipp 1971).

Distribution

Argentina, Belize, Bolivia, Brazil, Colombia, Costa Rica, Cuba, Curaçao, Ecuador, El Salvador, Guatemala, Guyana, Honduras, Jamaica, Mexico, Nicaragua, Panama, Perú, Uruguay, USA (Florida), Venezuela. (Fig. 42).

Distribution (bibliographic references)

Hitchcock (1911); Hitchcock (1913) as *L. liebmanniana* (Four.) Hitchcock; Hitchcock and Chase (1917); Hitchcock (1920, 1927a, 1930); Standley and Calderón (1925); Standley (1937); Swallen (1931, 1934, 1936, 1943, 1955b); Pinto-Escobar (1966); Adams (1972); Beetle (1977); Fournet (1978); Steyermark and Huber (1978); Davidse (1978, 1994, 2001, 2003, 2007); Pohl (1980); Wiggins (1980); Gould and Moran (1981); MacVaugh (1983); D'Arcy (1987); Cialdella and Vega (1996); Renvoize (1998); Morales (2003); Zuloaga et al. (2003); Correa et al. (2004); Renvoize et al. (2006); Rodriguez et al. (2006); Davidse et al. (2007); Sutherland (2008); Hokche et al. (2008); Catasús-Guerra (2012a); Acevedo-Rodríguez and Strong (2012); Rebman et al. (2016); Villaseñor (2016); Arrieta Herrera and Peterson (2018); Dávila et al. (2018); Sánchez-Ken (2019); Menjivar et al. (2021).

Ecology

Deciduous and semi-deciduous forests, coastal vegetation, edges of sandy savannas, associated with shrubs. From sea level up to 1600 m [cf. Costa Rica: Nayarit, *M. de J. Sepulveda S. 558* (MO)].

Phenology

June through February.

Remarks

Davidse (1978) cites as holotype the specimen P00128868, not reporting the other three specimens, all original material (P00128869, P00128870, P00128871). The fertile specimen (P00128869), here selected and designated as the lectotype matches better with the protologue (Kunth 1816) and the original description.

Figure 42. *Lasiacis ruscifolia* (Kunth in F.H.W. von Humboldt, A.J. Bonpland & C.S. Kunth) Hitchc.: general geographic distribution.

Lasiacis ruscifolia is closely related to *L. maculata* and the two species are often confused. *Lasiacis ruscifolia* is distinguished in having extremely broad ovate leaves, short ligules, and dense panicles with globose spikelets. The pubescence of the leaves is very variable from glabrous to densely pubescent plants in the same population (*pers. obs.* in Panama and El Salvador). The leaf width can range from 1 cm [*J.D. Dwyer 2598* (MO)] to 5 cm [*E. Asplund 5807* (FI, G, NY, P, UPS, US)]. The morphological polymorphism exhibited by this species has probably led to the high number of synonyms. Direct examination of the types states its gradual variation difficult to be expressed taxonomically either at species or infraspecific level. *Lasiacis ruscifolia* is widely distributed from the southern USA (Florida) throughout Central America and West Indies to South America to Argentina, one of the most widespread species in the genus. Beetle (1977) considered the synonym *L. globosa* as distinct species.

Selected specimens

ARGENTINA. **Misiones**. Matto Quemado, (Alto Uruguay), 27 Jan. 1947, *B.S. Bertoni 3231* (P); Misiones, Iguazu, 25-30 Jun. 1963, *Del Puerto & Brescia 2648* (US); Misiones, Iguazú, Puerto Bosetti, 13 Mar. 2003, *H.A. Keller & F. Moskovich 2100* (G).

BELIZE. **Cayo**. Central Farm, Sep. 1964, *R.H.L. Disney A380/D.2* (BM); El Cayo, Xunantunich, 2 Dec. 1968, *R.R. Innes 92* (K); Altun Ha, 24 Aug. 1970, *J.R. Wiley 562* (US); Belize Dustr., mile 42.5 on Northern Highway, N of Maskall River, 7 Jun. 1973, *J.D. Dwyer 11005* (MO); **Corozal**. Port Sal, Aug. 1933, *P.H. Gentle 104* (P); **Orange Walk**. Between Orange Walk and San Roman, 20 Aug. 1980, *C. Whitefoord 2138* (BM, MO); Orange Walk, New River Lagoon, 13 Sep. 1992, *C. Whitefoord 8163* (BM).

BOLIVIA. **Santa Cruz**. Prov. Andrés Ibáñez, 12 km E of center of Santa Cruz on road to Cotoca, 375 m, 17°46'S, 63°04'W, 9 Feb. 1987, *M. Nee 34030* (G, NY, US) .

BRAZIL. **Amazonas**. Río Branco, Serra do Mel, Aug. 1909, *E. Ule 8017* (G).

COLOMBIA. **Antioquia**. Medellín, 5 Dec. 1930, *W.A. Archer 756* (MA); Puerto Colombia, Oct. 1933, *Bro. Elias 1098* (G, NY); Amalfi, Veredas Chorritos, La Maria, Montebello, km 15-35 en la via a Chorritos-Los Monos, S-NE de Amalfi, 1180-1550 m, 06°40'N, 74°52'W, 6 Dec. 1989, *R. Callejas & al. 9014* (MO); **Bolívar**. La Popa, near Cartagena, 50-175 m, 2 Nov. 1926, *E.P. Killip & A.C. Smith 14082* (NY, US); Tierrabomba Island, Cartagena Bay, 4 Nov. 1926, *E.P. Killip & A.C. Smith 14126* (MO, US); N of Arjona, 30-50 m, 15 Nov. 1926, *E.P. Killip & A.C. Smith 14513* (NY, US); **Boyacá**. Santa Marta, 1898-1901, *H.H. Smith 174* (G, L, MA, MO, NY, P, US); **Cundinamarca**. Vicinity of Apulo, 455 m, 5 May 1944, *E.P. Killip & al. 38261* (US); Fusagasugá, 1952, *Køie s.n.* (C); **Guajira**. Barrancas, cercanias al Tajo Oeste, 3 Mar. 1980, *R. Fonnegra G. 1459* (MO); **Isla de San Andrés**. 15 Oct. 1956, *A. Fernandez-Pérez 5194* (US); Providence, near the airport (Bailey), 10 m, 2 Sep. 1985, *J.R.I. Wood 4734* (US); **Magdalena**. Magdalena, 24 Aug. 1943, *O.L. Haught 3633* (BM); Hoya del Río Cesar, Hoya del Río Azucarbuena, El Callao Region, Hacienda Santa Marta, 200 m, 30 Oct. 1959, *J. Cuatrecasas & R. Romero Castañeda 24922* (US); Pivijay, 22 Oct. 1961, *R. Romero Castañeda 9096* (MO); **Santander**. Vicinity of Suratá, 1700 m, 4-10 Jan. 1927, *E.P. Killip & A.C. Smith 16476* (NY, US); **Valle**. Alto del Dinde, entre Cartago y Alcalá, 1200-1260 m, 16 Nov. 1946, *J. Cuatrecasas 22909* (US).

COSTA RICA. **Alajuela**. Las Ventanas, Río Virilla, 31 Dec. 1950, *J. León 2926* (US); Zurrúcare arretnca del Río zigate, 600 m, 20 Sep. 1992, *C.O. Morales 414* (USJ); **Guanacaste**. Vicinity of Libano, 15 Jan. 1926, *P.C. Standley & J. Valerio 44888* (US); Bebedero, 3 Feb. 1926, *P.C. Standley & J. Valerio 46695* (US); 5-15 km S of La Cruz, 1 Jan. 1964, *L.O. Williams & al. 26436* (US); Savanna near Río Guajiniquil on Bahia de Sta. Elena, 5 Jan. 1964, *L.O. Williams 26703* (NY, US, W); Taboga, near Cañas, 13 Apr. 1966, *R.W. Pohl & C. Calderón 9826* (US); Along Carratera Interamericana, 21 km N of Liberia, *Curatella-Byrsonima* savanna, 75 m, 31 Jul. 1966, *R.W. Pohl & C. Calderón 10161* (USJ); 41 km NW of Liberia, along Carretera Interamericana, *Curatella-Byrsonima* savanna, 210 m, 2 Aug. 1966, *R.W. Pohl & C. Calderón 10192* (USJ); Nicoya Peninsula, hills near 27 Abril and along the road to Playa Tamarindo, 20-80 m, 10°16'N, 85°46'W, 28 Dec. 1966, *W. Burger & W. Ramirez 4117* (US); 5 km N of Cañas, Finca La Pacifica, 50 m, 24 Jun. 1968, *R.W. Pohl & G. Davidse 10541* (MO); 5 km N of Cañas, Finca La Pacifica, 25 Oct. 1968, *R.W. Pohl & G. Davidse 11335* (K, US); Puerto Castillo, 5 Dec. 1968, *R.W. Pohl & G. Davidse 11562* (K, US), **n = 18!** (Davidse 1978); Vicinity of Cañas, 12 Sep. 1969, *R. Daubenmire 169* (USJ); Hacienda Santa Rosa, 20 Jul. 1971, *R. Callaway 10898* (USJ); About 8 km N of Liberia, 10°42'N, 85°27'W, 2 Aug. 1971, *W.C. Burger & M. Burger 7855* (NY); Hacienda Santa Rosa, 1972, *M. Montiel 20* (USJ); Orilla del camino a Playa Naranjo, Parque Nacional Santa Rosa, 1 Aug. 1974, *J. Gómez Laurito 136* (USJ); Parque Nacional Santa Rosa, 12 Oct. 1974, *J. Gómez Laurito 258* (USJ); Along the Río Corobici about 4 km NW of Cañas, 4 Jan. 1975, *J. Taylor 18043* (US); Santa Rosa National Park, along dried up stream below Nature Trail, 100 m, 10°50'N, 85°37'W, 23 Jan. 1978, *R. Liesner 4422* (MO); Santa Rosa National Park, 15 Jul. 1989, *D.G. Furth 10* (MO); Area Conservacion Tempisque, Estación Palo Verde, bosque secondario, 10-100 m, 10°20'00"N, 85°21'10"W, 12 Dec. 1990, *U. Chavarria 208* (MO); Parque Nacional Santa Rosa, 15 Jul. 1992, *J.R. Grant & J.R. Rundell 92-01974* (MO, NY); Colorado de Abangares, 21 Oct. 1993, *R. Chacón 75* (K); Cañas, 10°42'N, 85°25'W, 11 Nov. 1994, *V. Nilsson & R. Manfredi 536* (K); Curù, road to Punta Quesera, 0-200 m, 9°46'N, 84°54'W, 16 Aug. 1995, *A.C. Sanders & al. 17582* (MO); Cantòn de Bagaces, Cuenca del Tempisque, 10°20'40"N, 85°20'28"W, 9 Dec. 1996, *A. Rodriguez 1801* (NY); San Miguel, Laguna de Aramuaca, 22 Jan. 1999, *R. Villacorta & al. 2693* (BM); Cantón de Bagaces, Cuenca del Tempisque, 10 m, 10°21'00"N, 85°17'55"W, 8 Dec. 1999, *L. Acosta 188* (MO, NY); Bagaces, Parque Nacional Palo Verde, Cuenca del Tempisque, Estación Palo Verde, Camino a Sendero Las Colmenas, 10 m, 10°21'55"N, 85°22'40"W, 7 Dec. 1999, *J.L. Chaves & al. 15* (MO); **Puntarenas**. 26 Oct. 1911, *A.S. Hitchcock 8570* (US), *8571* (NY, US), *8577* (NY, US), *8581* (US); 3 km E of Barranca, 22 Oct. 1968, *R.W. Pohl & G. Davidse 11278* (K, US), **n = 18!** (Davidse 1978); Islas San Lucas, Golfo de Nicoya, 5-25 m, 9°57'N, 84°54'W, 18 Oct. 1984, *M. Grayum & al. 4157* (MO); Reserva Absoluta Cabo Blanco, Estación Cabo Blanco, 20-100 m, 9°35'N, 85°06'W, 4 Nov. 1991, *U. Chavarria 287* (MO); Cantón de Aguirre, Cuenca del Naranjo y Paquita, Quebrada Grande Y Río Cotos, 30 Dic 1997, *J. Morales 6336* (K); Puntarenas, Chomes, 10°7'15"N, 84°53'2"W, 14 Jan. 2002, *R. Chacón 383* (K); **San José**. 1 km SW of Chimiral, 10 km NE of San Isidro del General, 875-900 m, 14 Jul. 1966, *R.W. Pohl & C. Calderón 10048* (USJ); San José, Acosta, Cangrejal, 12 Dec. 2001, *J. Quesada 901* (K).

CUBA. In Cuba Orientali, 1856-57, *C. Wright 749* (G, MO); **Camaguey**. Palo Seco, in forest at foot of Loma decada, 3 Oct. 1922, *E.L. Ekman 15318* (NY, US); **Habana**. Road from El Caney to San Vicente, Santiago, Nov. 1947, *Bro. Clemente 5683* (US); **Nueva Gerona**. Isla de Pines, 14 Jan. 1904, *A.H. Curtiss 291* (NY), 31 May 1904, *A.H. Curtiss 520* (BM, G, K, L, MO, NY, P, US); Isle de Pines, Cerro San Juan del Mar, Columbia, 20 Feb. 1916, *N.L. Britton & al. 14659* (NY, US); Isle of Pines, Vivijagua, 28-29 Feb. 1916, *N.L. Britton & al. 15065* (US); Isla de Pines, Sierra de Casas, 18 Oct. 1920, *E.L. Ekman 11721* (K, NY, US); Isla de la Juventud, Sierra Las Casas, 28 Apr. 1954, *E.P. Killip 44165* (US); Woods at base of Sierra de Caballos, near Presidio, 19 Jan. 1955, *E.P. Killip 44533* (US); **Oriente**. Ensenada de Mora, 26-29 Mar. 1912, *N.L. Britton & al. 12979* (NY, US); S of Guantanamo, 4 Aug. 1913, *Bro. Léon 3778* (NY, US); Roja, 100 m, 5 Mar. 1915, *E.L. Ekman 4903* (US); Sabanaso, 27 Oct. 1915, *E.L. Ekman 6535* (BM, G, K, NY, US); Mir, 22 Aug. 1916, *E.L. Ekman 7578* (G); Santiago de Cuba, between Marimon et Boniato, in serpentine hills, 24 Nov. 1916, *E.L. Ekman 7699* (US); Guantanamo, Finca Forment, 14 Nov. 1918, *Bro. Horam 2240* (NY); **Pinar del Río**. Vicinity of Los Palacios, 8 Jan. 1912, *J.A. Shafer 11684* (NY).

CURAÇAO. Mt. Christoffel, 12 Mar. 1999, *van Proosdij & al. 1025* (K).

ECUADOR. **Guayas**. Oil Camp between Guayaquil and Salinas, 21-24 Jun. 1923, *A.S. Hitchcock 20057* (NY); Oil Camp between Guayaquil and Salinas, 22 Jan. 1923, *A.S. Hitchcock 20037* (US); Chongòn, 6 Mar. 1939, *E. Asplund 5208* (BR, FI, G, NY, P); Guayaquil, 13 Apr. 1939, *E. Asplund 5687* (BR); Guayaquil, 26 Apr. 1939, *E. Asplund 5807* (FI, G, NY, P, UPS, US); Sabanilla, 25-30 m, 12 Apr. 1951, *M. Acosta Solís 20582* (US); Capeira, km 21 Guayaquil to Daule, 20-200 m, 17 Sep. 1981, *C.H. Dodson & P.M. Dodson 11309A* (MO); Guayas, Guayaquil Canton, Bosque Protector Cerro Blanco, Carretera Guayaquil-Salinas, km 15, 100 m, 02°10'S, 79°50'W, 6 May 1992, *G. Tipaz & al. 803* (MO); **Loja**. 23 km NW of Chaguarpampa on road to Balzas and the coast, 600 m, 4 Jun. 1990, *P.M. Peterson & E.J. Judziewicz 9520* (MO); **Oro**. Bosque Petrificado Puyango, 80°05'W, 03°52'S, 7 May 1997, *B.B. Klitgaard & al. 517* (NY); **Pastaza**. Colonia 24 de Mayo, side road to road Puyo-Puerto Napo, 15-20 km NE of Puyo, 27 Jun. 1972, *H. Lugo S. 2497* (MO).

EL SALVADOR. **Ahuachapán**. Sierra de Apaneca, in the region of Finca Colima, 17-19 Jan. 1922, *P.C. Standley 20109* (US); Vicinity of Ahuachapán, 9-27 Jan. 1922, *P.C. Standley 19870* (MO, NY, US); Parque Nacional El Imposible, transecto 3, San Benito, 13°49'N, 89°56'W, 12 Dec. 1989, *A. Sermeño 33* (MO); San Francisco Menéndez, El Corozo, Mariposario, 12 Apr. 2000, 2 Jul. 1959, *C.L. Lundell 16106* (C, G); San Francisco Menéndez, El Corozo, Mariposario, 26 Sep. 2000, *J.M. Rosales 1495* (BM); Santa Rita, 20 m, 13°48'N, 90°04'W, 14 Jan. 2004, *J.M. Rosales 1870* (BM, MO); **Cuscatlán**. Cojutepeque a orillas de calle al Cerro de Las Pavas, 16 Jan. 1996, *R. Villacorta & E.A. Montalvo 2324* (K); **La Libertad.** 1.5 km E of Apulo along the N shore of Lago Olopango, 600 m, 7 Jun. 1970, *G. Davidse & R.W. Pohl 2033* (MO); La Libertad, San Diego, El Amatal, 21 Sep. 1997, *R. Aparicio & R. Rivera 15* (K); La Libertad, Cafetale de Miguel E. Araujo, 13°39'33"N, 89°22'49"W, 7 Feb. 1998, *A. Monro & al. 2267* (BM, MO); **La Unión.** Sierra de Conchagua, Gulf of Fonseca, 3 Dec. 1838, *Barclay s.n*. (BM); Vicinity of La Unión, 13-21 Feb. 1922, *P.C. Standley 20660* (US); La Unión, Isla Martin Perez, 11 m, 13°16'N, 87°44'W, 4 Dec. 2006, *D. Rodriguez 649* (MO); **Morazán**. Montecristo, ca. 15 km NE of San Miguel, 8 Dec. 1941, *J.M. Tucker 488* (K, US); **Santa Ana**. 15-18 Nov. 1911, *A.S. Hitchcock 8850* (K, NY, US); Santa Ana, San Miguel Ingenio, 11 km E of Metapán, 900 m, 11 Jul. 1971, *R.W. Pohl & L. Erickson 12583* (MO), **n = 18!** (Davidse 1978); Parque Nacional Montecristo, 14°21'58"N, 89°24'08"W, 936 m, 13 Feb. 2016, *J. Menjívar & R.M. Baldini 3691* (FT, LAGU, MHES, MO); **San Miguel**. Vicinity of San Miguel, 24-27 Feb. 1922, *P.C. Standley 21138* (US); **San Salvador**. Vicinity of Tonacatepeque, 30-31 Dec. 1921, *P.C. Standley 19421* (US), *19437* (NY); San Salvador, 1922, *S. Calderón 510* (NY, US); Lake Illopango, 500 m, 13°38'16"N, 89°3'23"W, 3 Feb. 1998, *K. Sidwell & al. 610* (BM, MO); **Sonsonate**. Nahuizalco, 12 Jan. 1898, *C.V. Hartman 50* (FI); 28 Nov. 1911, *A.S. Hitchcock 8979* (US), *8982* (NY, US); Santa Isabel Ishuatan, cerca del puente, el Ecuador, 430 m, 13°41'N, 89°33'W, 6 Nov. 2005, *D. Rodriguez 158* (MO); **Usulután**. Puerto El Triunfo, caserio Ceiba doblada, 10 m, 13°12'N, 88°37'W, 26 Aug. 2003, *R.A. Carballo 888* (MO).

GUATEMALA. **Alta Verapaz**. 1906, *H. von Türckheim 809* (FI, L); Alta Verapaz, along access road to Finca Argentina above Papalha, 15 miles W of Teleman, 250 m, 19 Jul. 1977, *T.B. Croat 41532* (MO); **Baja Verapaz**. Salamá, 4 Dec. 1896, *E. Seler 2446* (US); Salamà Puente Barranca, al W de Salamà, 820 m, 15°06'N, 90°18W, 24 Jul. 1988, *P. Tenorio L. 14739* (MO); **Chiquimula**. Grassy plains and low slopes around Chiquimula, 400 m, 20 Oct. 1939, *J.A. Steyermark 30083* (US); **El Progreso**. San Cristobal Acasaguastlan, 200-300 m, 14°55'20"N, 89°49'20"W, 4 Oct. 2003, *A. Cóbar 998* (MO); **Guatemala**. From Guatemala City to El Chol, 850 m, 14°52"N, 90°37'W, 25 Jan. 1987, *T.B. Croat & D.P. Hannon 63555* (K, MO); **Huehuetenango**. Trail between Nentón and Catarina, Sierra de los Cuchumatanes, 800-900 m, 3 Sep. 1942, *J.A. Steyermark 51810* (US); Río Azul, Nenton, 670 m, 15°45'35"N, 91°50'W, 5 Dec. 2006, *M. Garcia 2220* (MO); **Izabal**. Vicinity of Lago Izabal, shore of Río Sauce, 2 km N of Lake Izabal, E of El Estor, sea level, 89°0'-89°25'N, 15°15'-15°35'W, 1966, *G.C. Jones & L. Facey 3054* (USJ), *3474* (US); Lake Izabal, 22 May 1966, *S.C. Snedaker D 51* (NY); **Jalapa**. Mountains along the road between Jalapa and San Pedro Pinnula, 1400-1800 m, 12 Nov. 1940, *P.C. Standley 77080* (US); **Jutiapa**. Between Jutiapa and Las Tunas, NW of Jutiapa, 850-900 m, 4 Nov. 1940, *P.C. Standley 76224* (US); **Petén**. Yaxha-Remate Road, 16 Jun. 1933, *C.L. Lundell 3862* (US); Lake Petén Itza, along north shore, W of San Andres, 22 Jan. 1962, *C.L. Lundell 17240* (US); North Shore Lake Petén, 19 Jun. 1973, *J.D. Dwyer 11274* (US); Just N of El Cruce on road to Tikal, 19 Jun. 1973, *A. Gentry 8319* (US); 2 miles E of Melchor, 16-18 Jun. 1973, *T.B. Croat 24618* (K); SE part of Cerro Cauhui, 20 Apr. 1986, *R.L. Walker 1244* (MO); Lago Petén Itza' ca. 1 km NNE-NE zentrum von San José, 115 m, 16°59'16-25"N, 89°53-54'W, 19 Aug. 1993, *B. Wallnöfer & F.M. Tut-Tesucun 5958* (MO); **Retalhuleu**. Along Río Coyote, W of Retalhuleu, 300 m, 24 Feb. 1941, *P.C. Standley 88381* (US); **Santa Rosa**. Jumaytepeque, Aug. 1892, *E.T. Heyde & Lux 3899* (BM, G, US); **Suchitepéquez**. Cocales, 5 Jan. 1939, *P.C. Standley 62085* (US); **Zacapa**. Rocky hills in vicinity of Santa Rosalia, 2 miles S of Zacapa, 200 m, 7 Oct. 1939, *J.A. Steyermark 29294* (US); Zacapa, between Río Hondo and Santa Cruz, 11 Oct. 1940, *P.C. Standley 74114* (K).

HONDURAS. **Atlantida**. Vicinity La Ceiba, Mt. Cangrejal, 5 Jul. 1938, *T.G. Yuncker & al. 8226* (BM, G, K, MO, NY); Lancetilla Valley, near Tela, 6 Dec. 1927–20 Mar. 1928, *P.C. Standley 52803* (US); Lancetilla Valley, 22 Jun.-27 Jul. 1929, *A.M. Chickering 9* (US); Ca. 8 miles W of Tela along the Highway to El Progresso, 40 m, 15°45'N, 87°33'W, 18 May 1991, *G. Davidse & al. 34518* (MO); 33 km SE of Tela by road in Valley of Río Lean, 20 m, 26 Jun. 1970, *G. Davidse & R.W. Pohl 2190* (MO); **Comayagua**. San Patricio, orilla del Río Yure, 200 m, 6-15 Feb. 1981, *C. Nelson*

& al. 7474 (MO); **Copán**. Along Copán River, vicinity of Copán Ruins Town, 18 Nov. 1969, *A. Molina & A. Molina 24610* (NY); On thickets of Copan River vicinity Jaguar Temple of Copán, 600 m, 3 Jan. 1990, *A. Molina R. & A.R. Molina 34262* (MO); **Córtes**. 10 Aug. 1961, *J. Dickson 271* (FTG); 1 km S of Puerto Cortés, 50 m, 23 Jun. 1970, *G. Davidse & R.W. Pohl 2169* (K, L, MO, NY, US); Aldea La Pita, 5 km SO de Puerto Cortes, 26-30 Nov. 1975, *C. Nelson & al. 3021* (MO); S of Villanueva, 24 Sep. 1991, *M. Chorley 407* (BM, MO); 2 km S of Omoa, 20 May 1987, *S. Blackmore & M. Chorley 4000* (BM); **El Paraiso**. 8 km W of Oyo de Agua, 27 Oct. 1946, *L.O. Williams & A. Molina 10736* (US); Drainage of the Río Yeguare, 24 Aug. 1948, *A. Molina 1085* (US); Entre Mata Indio y Lizapa, drainage of the Río Yeguare, 25 Jul. 1951, *A. Molina 4051* (US); Along Highway 17, 9 km S of Danlí, 760 m, 30 Dec. 1977, *R.W. Pohl & M. Gabel 13424* (MO); **Islas de La Bahia**. Between Coxenhole and Flowers Bight Roatán Island, 20 Apr. 1967, *A. Molina 20662* (NY, US); Islas de La Bahia, camino entre ciudad de Roatan y Fowers Bay, 10-13 Apr. 1974, *C. Nelson 2087* (MO); **Morazán**. Río Yeguare Valley, in forest along Santa Clara Creek, 800 m, 18 Aug. 1946, *L.O. Williams & A. Molina R. 10343* (MO); Río de La Orilla, SE of El Zamorano, base of Cerro Majicarán, Nov. 1948, *P.C. Standley 15177* (P); El Zamorano, along the road toward San Antonio de Oriente, 9 Aug. 1949, *P.C. Standley 22316* (P); In barranco between Las Mesas and Sta. Clara Creek, 3 Sep. 1949, *L.O. Williams 15956* (US); Vine in tree on slope of Cerro Majicoran above Río de la Orilla, 16 Oct. 1949, *L.O. Williams 16928* (USJ); El Zamorano, above Agua Amarilla, Oct.-Nov. 1948, *P.C. Standley 26683* (US); Morazán, vicinity El Zamorano, 22 Oct. 1951, *J.R. Swallen 11008* (P, US); El Zamorano, Aug. 1960, *H.W. Pfeifer 1622* (US); SE of Tegucigalpa, edge of moist thicket of Río Rancho Quemado, 20-25 km road to Sabana Grande, 9 Nov. 1966, *A. Molina 18651* (G); 8 km E of El Zamorano, 700 m, 14 Jun. 1970, *G. Davidse & R.W. Pohl 2082* (MO); Orillas del Río Choluteca, al S de Tegucicalpa, 950 m, 30 Aug. 1981, *T.M. Mejia Ordonez 36* (MO); Tegucigalpa, Colonia La Primavera, 950 m, 3 Sep. 1981, *J.C. Soto 75* (MO); Occasional in garden of vegetable shop of EAP El Zamorano, 800 m, 1 Jul. 2001, *A. Molina R. & A.R. Molina 35161* (MO); San Antonio de Oriente, loc. Quebrada El Gallo, a orillas de la quebrada, 940 m, *J. Araque 977* (MO); **Ocotepeque**. El Cerro, vicinity of San Antonio, 30 Aug. 1968, *A. Molina 22466* (NY); **Olancho**. Along Río Olancho, W of main Tegucigalpa-Catamas Highway, ca. 1 km upstream from and NW of Puente Boquerón, 8.6 miles SW of Catacamas, 6 miles SW of Santa Maria del Real, 400 m, 14°45'N, 86°00'W, 4 Feb. 1987, *T.B. Croat & D.P. Hannon 64094* (MO); **Santa Bárbara**. San Pedro Sula, Jul. 1888, *C. Thieme 5585* (K, US); Aldea San Miguel, 5 km al N de Colinas bosque húmedo subtropical, 23 Jan. 1984, *R. Paz 168* (NY); **Valle**. Amapala, 12 Nov. 1911, *A.S. Hitchcock 8763* (US); Amapala, 12 Sep. 1945, *V. Rodriguez 3422* (US).

JAMAICA. **St. Andrew**. Below Flamstead, 26 Nov. 1912, *W. Harris 11469* (P); Blue Mts., Robertsfield, 3 Dec. 1912, *W. Harris 11491* (P); **St. Elizabeth**. Near Black River, Font Hill, 18 Sep. 1907, *N.L. Britton 1509* (NY); **Westmoreland**. Bluefields and vicinity, 22 Sep. 1907, *N.L. Britton 1624* (NY).

MEXICO. **Apatzingán**. Aguililla, 12 Sep. 1939, *G.B. Hinton 15156* (W); **Baja California**. Arroyo Hondo, near base of cliffs on north side of Cerro de la Giganta, 24 Nov. 1947, *A. Carter & L. Kellogg 2023* (K, US); Baja California, Cañon del Cayco, east base of Cerro de la Giganta, Sierra de la Giganta, 7 Oct. 1951, *A. Carter & L. Kellogg 3110* (US); Mexico, Baja California Sur, Unknown, Sierra de la Giganta; Arroyo Tabor., 25.7981 -111.3483, 150m, 7 Oct. 1970, *R. Moran 18223* (SD); Baja California Sur, La Paz, Sierra La Gata: southeast of San Juan de Los Planes and north of San Bartolo; along canyon & trail to the east of Rancho Palo Verde, 23.82594 -109.87641, 615 m, 8 Nov. 2016, *J. Rebman 32016* (SD); **Campeche**. 28 km N of Escárcega, 7 Mar. 1982, *E. Cabrera 2032* (BM, MO); Campeche, 18°32'14"N, 89°53'52"W, 11 Apr. 1995, *P. Zamora 4866* (NY); Campeche, Calkmul, a 9 km al E de Constitucion, 150 m, 18°38'48"N, 90°15'45"W, 11 Dec. 1998, *E. Martinez S. 31694* (MO); **Chiapas**. Escuinula, 1937, *E. Matuda 2117* (K, NY, US); Santa Rosa, Río de la Cruz, E of Taxisco, 2 Dec. 1940, *P.C. Standley 79009* (K); 14 miles E of Cintalpa, 28 Aug. 1953, *J.R. Reeder & C.G. Redeer 2137* (US); Mapastepec, 30 Oct. 1960, *T. Tateoka 1001* (US), **n = 18!** (Tateoka 1962); S of Sureste on road to Mal Paso, 17°15'N, 93°35'W, 24 Aug. 1965, *K. Roe & al. 1432* (BM, US); La Trinitaria, along Highway 190, 11 miles S of La Trinitaria, 14 Oct. 1965, *D.E. Breedlove & P.H. Raven 13247* (US); Venusiano Carranza, at Rancho Nacimiento along the road between Chiapilla and San Lucas, 23 Feb. 1966, *R.M. Laughlin 277* (US); Venustiano Carranza, along the road from Acala to Pugiltil, 7 Nov. 1967, *A.S. Ton 3180* (NY, US); Chiapa de Corzo, El Chorreadero, 28 Nov. 1967, *A.S. Ton 3269* (NY); Tonalà, NW side of Cerro Veronal, 25-30 km SE of Tonalà, 400-600 m, 4 Oct. 1972, *D.E. Breedlove 28329* (MO, NY); 14,8 miles S of Ocozocoautla on Highway 190, 9 Oct. 1976, *J. Brunken & C. Perino 316* (US); Primeiro de Guillén, Tuxtla Chico, 9 Oct. 1984, *E. Ventura & E. López 443* (BM); Tuxtla Gutierrez, El Zapotal, 25 Dec. 1984, *C. Cowan 5029* (MO, NY); Chiapas, Tuxtla Chico, 29 Jul. 1985, *E. Ventura & E. López 2156* (BM); Porvenir, Mun. de Tapachula, 28 Oct. 1985, *E. Ventura & E. Lopez 2606* (G, P); Chicoasen, Mirador "Manos que Imploran", 10 km al S de Chicoasen, 700 m, 8 Nov. 1988, *A. Reyes-Garcia 1147* (MO); 32 km S of Tuxtla Gutierrez, on road to Suchiapa, 19 Jul. 1990, *R.J. Hampshire & A. Reyes García 1295* (BM, MA); Arriaga, 19 Oct. 1990, *J.C. Soto & al. 13209* (BM); Ocosingo, NE del poblado Nuevo Guerrero, 17°0'0N, 91°45W, 13 Jul. 2003, *G. Aguilar M. 7385* (P); **Chihuahua**. 1885, *E. Palmer 10* (BM, K, NY, P, NY); Guasaremos, Río Mayo, 20 Aug. 1936, *A. Gentry 2402* (K, MO); **Chiquimula**. Between Ramírez and Cumbre de Chiquimula, 15 Oct. 1940, *P.C. Standley 74531* (K); **Colima**. Alzada, 21 Sep. 1910, *A.S. Hitchcock 411* (BM, C, L, MO, NY, P, US, W), *414* (BM, G, K, L, MO, NY, US, W); About 17 miles S of Colima, 19 Sep. 1953, *J.R. Reeder & C.G. Redeer 2373* (MO, US); Mountain summits near pass ca. 11 miles SW of Colima on Manzanillo road, 21 Sep. 1958, *R. McVaugh 18051* (US); About 14 miles N of Manzanillo on the road to Minatitlan on steep slopes with tropical vegetation, 24 Sep. 1974, *J.R. Reeder & C.G. Redeer 6345, 6346* (US) **2n = 36!** (Reeder 1967); **Durango**. Near Huasemote, 15 Aug. 1897, *J.N. Rose 3502* (K, US); **Guerrero**. Acapulco, 1894/95, *E. Palmer 115* (BM, K, MO, NY, US); El Calabazal, 15 Oct. 1898, *E. Langlassé 458* (G, P, US); Temisco, Barranca de la Julia, 1 Nov. 1937, *Y. Mexia 8717* (BM, G, K, MO, NY, US); Beyond Acahuizotla, on Highway to Acapulco, 30 Sep. 1949, *H.E. Moore 5107* (BM, C, G, US); In open pine-oak forest along road from Almoloya-Teloloapan-Iguala, 10 Oct. 1953, *E.R. Sohn 966* (K, US); 9 miles SW of Tierra Colorado, 14 Nov. 1964, *J.R. Reeder & C.G. Reeder 4156* (US); Est edge of beach at Puerto Marques, just E of Acapulco, 23 Nov. 1975, *A. Lasseigne 4966* (MO, NY); Atoyac, carretera a El Paraiso, 21 km al NE de Atoyac, cerca de Río Santiago, 720 m, 3 Nov. 1979, *S.D. Koch & al. 79302* (MO); A 2 km al NE de Guayameo, camino Zirandaro-Guayameo, 720 m, 13 Jul. 1982, *E.M. Martinez S. 1359* (US); Petatlán, En Rancho Alegre, 4 km al de Coyuquilla, 23 Oct. 1985, *J.C. Soto & al. 11346* (MA, US); Petatlán, NE de Coyuquita, camino al Porvenir, 23 Oct. 1985, *J.C. Soto & al. 11337* (MA); 16 km al N del Ocotito, carretera Tierra Colorada-

Chilpancingo, 4 Dec. 2004, *R. Torres C. 16788* (HUEFS); **Jalisco**. Guadalajara, near Río Grande de Santiago, 26 Aug. 1941, *W. & M. Leavenworth 1901* (MO, NY); 18 miles NW of Magdalena, 21 Sep. 1953, *J.R. Reeder & C.G. Redeer 2399* (MO, US); Steep rocky mountainsides, on limestone, 8 miles SW of Pihuamo, 6 Dec. 1959, *R. McVaugh & W.N. Koelz 1498* (G); 16 miles SW of Autlan, 7 Oct. 1960, *R. McVaugh 19975* (US); Playa de Cuastecomate, 8 km road NW of Barra de Navidad, 6 Nov. 1960, *R. McVaugh 20761* (NY, US); Hills between Bahia Navidad, and La Manzanilla on Bahia Tenacatita, east-facing summits 3 miles W of the Autlan-Navidad Highway, 12 Nov. 1960, *R. McVaugh 21022* (US); Wooded hills 2 miles above, N of, La Cuesta, road La Talpa de Allende, 19 Nov. 1960, *R. McVaugh 21144* (NY, US); 2 km S de Puerto Vallarta, 11 Nov. 1963, *J. Rzedowski 17729* (US); About 2 km N of Puerto Vallarta, 13 Nov. 1963, *C. Feddema 2544* (NY, US); 2-6 km SE of La Manzanilla, above Bahia Tenacatita, 6 Dec. 1970, *R. MacVaugh 25036* (NY, US); Puente Hidalgo, crossing of Río Grande de Santiago on the Guadalajara-Zacatenas Highway, 1200 m, 20°50'N, 103°21'W, 15 Aug. 1973, *M.C. Johnston & al. 12243* (MO, NY); Ca. 6 miles N of La Resolana (Casimiro Castillo) on route 80, 11 Oct. 1976, *T.F. Stuessy & R.C. Gardner 4140* (MO); Puerto Vallarta, ca 5 km W of the center of town, 175 m, 6 Nov. 1983, *R. Soreng 2185* (US); 2 km W of La Palomita on road to El Divisadero, ca. 23 km ESE of Tomatlan, 19°52'N, 105°02'W, 14 Jan. 1979, *H.H. Iltis & M. Nee 1620* (MO, US); 10 km E of Villa Corona on Highway 80, 16 Sep. 1983, *W.R. Anderson 12668* (NY); El Limon, La Tabaquera, 2.5 km al W de El Limon, por carretera a El Grullo, 950 m 11 Oct. 1986, *F.J. Santana & al. 2261* (MO); El Limón, Rancho El Recodo 2 km al E de San Miguel Hidalgo, 1 Oct. 1987, *F.J. Santana 2960* (NY); La Huerta, Rancho Cuixmala, 19°26'N, 104°59'W, 3 Nov. 1991, *E.J. Lott 4003* (US); **Michoacan**. From El Temascal, on road to Heutamo, 12 Nov. 1949, *H.E. Moore & al. 5665* (BM, US); Old lava flows 4 miles NW of Apatzingán, 16 Sep. 1958, *R. McVaugh 17925* (G, NY, US); West facing slopes of Sierra Madre del Sur, ca. 22 kms N of Playa Azul, region of Los Encinos, 25-31 Oct. 1961, *R.M. King & T.R. Soderstrom 4925* (NY, US); Mugica, along the autopista Labaro Cardenas-Morelia, 5.5 km NE of the exit for Nueva Italia, just W of the Río El Marqués, 19°01'44"N 102°03'19"W, 2 Sep. 2001, *V.W. Steinmann 1913* (NY); **Morelos**. Near Yautepec, 3 Oct. 1902, *C.G. Pringle 11293* (K, MO, US); Xochitepec, 24 Sep. 1938, *E. Lyonnet 2658* (BM); **Nayarit**. Maria Madre, Tres Marias Islands, 23 Oct. 1925, *R.S. Ferris 5656* (US); Road from Tepic to Compostello, 13 Sep. 1926, *Y. Mexia 597* (BM); About 50 miles NW of Tepic, 23 Sep. 1953, *J.R. Reeder & C.G. Reeder 2423* (MO, US); On the bajada, ca. 19 miles NW of Tepic, Highway to Mazatlan, 15 Nov. 1959, *R. McVaugh & W.N. Koeltz 722* (US); Valle de Bandeiras, 1 km al N de El Cuatante, 18 Nov. 1963, *J. Rzedowski 17880* (US); Pochotitlan, 15-20 km al E de Francisco I. Madestro, 4 Oct. 1987, *O. Téllez V. 10788* (NY); Ixtlan, 5-6 km de la terraceria a Cascalutan, 1100 m, 21°05'N, 104°17'W, 22 Sep. 1989, *O. Tellez V. 12323* (MO); Nayar, km 2-4 de la vereda de la Mesa del Nayar al Cangrejo (Villa de Guadalupe), cruzando el barranco, 900-1200 m, 20 Oct. 1989, *O. Tellez V. 12462* (MO); Nayar, P.H. Aguamilpa aprx. A 20 km al SE de la Cortina o a 5 km al N del poblado Colorado de la Mora, 200 m, 21°43'N, 104°39'W, 5 Oct. 1993, *F. Franco & al. 2975* (MO); **Oaxaca**. Dec. 1900, *C. Conzatti 1103* (US); Vicinity of Cafetal Concordia, 1-15 Apr. 1933, *C.V. Morton & Makrinius 2441* (K, US); Villa Alta, from Temascalpa to San Ildefonso de Villa Alta, 29-30 Oct. 1944, *J.V. Santos 3534* (NY, US); 11 miles W of Zanatepec, 28 Aug. 1953, *J.R. Reeder & C.G. Reeder 2156* (US); Chiltepec, Tuxtepec, 15 Jul. 1965, *G.M. Calderón 120* (MO, NY); Barranca de Río Grande on road to San Lorenzo, near Mitla, 22 Jan. 1966, *W.R. Ernst 2285* (US); Jamiltepec, 3 km NE of Flores Mágon, 18 Nov. 1982, *P. Tenorio & al. 2725* (BM); Tuxtepec, Mun de Soyaltepec, N end of eastern dam, 2 km N of Hidroelectrica Temascal, 60 m, 18°14'N, 96°23'W, 21 May 1986, *R.E. Gereau & al. 2235* (MO); Uxpanapa Region, along gravel road between Esmeralda and Río Verde, 1.1 miles S of Esmeralda, 100 m, 17°10'N, 94°45'W, 19 Jan. 1987, *T.B. Croat & D.P. Hannon 63308* (MO); Tehuantepec, Santo Domingo, 16°1'16"N, 95°25'14"W, 31 Aug. 1999, *J. Rivera & al. 1847* (NY); Pochutla, San Miguel del Puerto, Zimatàn, 15°56'10"N, 96°2'30"W, 24 Sep. 1999, *C. Perret & al. 532* (NY); Tehuantepec, Santiago Astata, Los Guayacanes, E de la Brecha a Chacalapa, 15°53'28.3"N, 95°55'14.6"W, 26 Oct. 2001, *S.H. Salas & al. 4213* (P); **Quintana Roo**. Tancah, 4-5 Aug. 1932, *J.R. Swallen 2808* (US); En San José, a 8 km al S de la carretera Chetumal-Escarcega, sobre camino a Tomas Garrido, 5 Sep. 1980, *O. Tellez & L. Rico 3368* (MO); San Felipe Bacalar, 57 km N of Chetumal on road to Cancún, 8 May 1982, *G. Davidse & al. 20213* (BM, MO); **San Luis de Potosí**. Tamazunchale, 7 Nov. 1937, *M.T. Edwards 478* (BM, MO, US); In a tropical forest between Narango-Platinito-Salto de Agua, 22 Sep. 1954, *E.R. Sohns 1408, 1417* (K, US); **Sinaloa**. Mazatlan, Sep. 1932, *J.G. Ortega 7058* (BR, G); Sinaloa, Imala, 19 Nov. 1939, *H.S. Gentry 4981* (MO, US); Cerro Llano Redondo, W of Caymanero, 8 Oct. 1944, *H.S. Gentry 7097* (NY, US); Along the road to Micro Ondas La Palma, 1,3 miles E of Mexico Highway 15, this road junction at km 225, about 26 miles S of Mexico Highway 40 junction S of Mazatlan and about 1,5 miles N of Rosario, 6 Oct. 1975, *J.L. Reveal & R.M. Harley 4020* (MO, US); Along the dirt road from Rosario to Plomosas, 8 Oct. 1975, *J.L. Reveal & R.M. Harley 4061* (K, MO, NY, US); Above La Reforma, 6 Nov. 1977, *M. Kimnach & al. 2022* (US); **Sonora**. SW slopes of Babiso Mts., 18 miles SE of Magdalena, 12 Sep. 1934, *I.L. Wiggins 7148* (US); Mescales, Río Mayo, 21 Jul. 1936, *A. Gentry 2290* (K, MO); Ravines and slopes of the Sierra Batuc, 8 miles NE of Matape, between Matape and Batuc, 9 Sep. 1941, *I.L. Wiggins & R.C. Rollins 430* (MO, NY, US, W); 13 miles W of Santa Ana on old road to Yécora, 22 miles E of Nuri, 9 Oct. 1976, *R. Spellenberg 4596* (NY); **Tabasco**. La Palma, 1 Jun. 1939, *E. Matuda 3292* (US); Ca. 21 km W of Cardenas, 15 Aug. 1974, *J. Conrad & R. Conrad 2966* (K, MO); **Tamaulipas**. Vicinity of Marmolejo, 2 Aug. 1930, *H.H. Bartlett 10796* (NY, US); Tampico, 28 Jul. 1946, *G.L. Fisher 46193* (US); Between La Concepcion and Aldama on the Aldama-Soto, la Marina Road, 27 Sep. 1956, *F.M. Martinez 2182* (US); Top of Mesa de Llera, 35 miles by Highway S of Victoria, 26 Sep. 1960, *M.C. Johnston 5754* (US); Aldama, ca. 40 km NE of Aldama near Barra del Tordo, 97°2'W, 23°45'N, 21 Sep. 1981, *P.A. Fryxell 3696* (NY); **Temascaltepec**. Plaza de Callos, 18 Sep. 1932, *G.B. Hinton 1767* (G, NY, US); Tenayac, 28 Sep. 1933, *G.B. Hinton 4847* (BM, NY, US); **Veracruz**. San Antonio, 1 Jan. 1926, *G.J.N. Woronow 2182* (US); Misantla, Aug. 1912, *C.A. Purpus 5978* (BM, G, L, MO, NY, US, P); Region of San Andrés Tuxtla, 7 Aug. 1953, *R.L. Dressler & Q. Jones 5* (BM, NY, US); La Laja, 14 Nov. 1963, *H.S. McKee 10955* (P); Michoacan, Chila, 8 km NW de Aquila, 23 Nov. 1963, *J. Rzedowski 17932* (US); 1 mile E of Santiago Tuxtla, 8 Aug. 1965, *J.R. Reeder & C.G. Reeder 4333* (US), **2n = 36!** (Reeder 1967); Tlaliscoyan, 20 Nov. 1967, *G.M. Calderón 1561* (BM, NY); Catemaco, 24 Sep. 1971, *J.I. Calzada 534* (BM, MO); Catemaco, E side of entrance of Laguna de Sontecomapan into Gulf of Mexico, 7 km of Sontecomapan, 18°33'30"N, 94°59'W, 1 Nov. 1981, *M. Nee 22602* (MO, NY); Puente Nacional, 6 km SW of Conejos junct., Conejos-Totutla Highway, 19°17'N, 96°32'W, 13 Nov. 1981, *M. Nee 23073* (MO, NY); **Yucatán**. Izamal, 1895, *G.F. Gaumer 878* (C, G, MA, MO, NY, P, UPS, US, W); Chichen Itza, 7-13 Jul. 1932, *J.R. Swallen 2396, 2398, 2418* (US); Uxmal, 20-21 Jul. 1932, *J.R. Swallen 2635* (K); Peto, 16-27 Jul. 1932, *J.R. Swallen 2694, 2717* (US); Uxmal, 29 Sep. 1959, *O. Degener & I. Degener 26760* (NY, US, W); Mayacan, 24 Jan. 1971, *A.A. Beetle 957* (US); Vicinity of grutas above Calcehtok, 16 Jul. 1982, *D.A. White 205* (NY); Vallaloid, Xuilub, 25 m, 88°04'W, 20°23'N, 14 Oct. 1989, *B. Mogensen 1143* (MO, NY); Yucatán, Uxmal, 30 m, 6 Oct. 1995, *M. Piepenbring 1865* (USJ); Sotuta, Cenote Xmucuy, Sotuta-Tixcacaltuyub, 20°33'32"N, 88°59'47"W, 24 Sep. 1996, *C. Espadas & al. 106* (NY); Entrada a Izamal, 20°56'44.5"N, 89°04'20.9"W, 10 m, 13 Oct. 2010, *J.E. López Contreras 1083* (G).

NICARAGUA. **Boaca**. 24 Jan. 1970, *F.C. Seymour 3841* (BM, MO, NY); 2 km al N de Boaquito, camino a Santa Lucia, 12°28'N, 85°44'W, 21 Oct. 1982, *P.P. Moreno 18123* (MO); **Carazo**. Jinotepe 3-7 Nov. 1911, *A.S. Hitchcock 8676* (NY, US), *8719* (K, NY, US); **Chinandega**. El Realejo, Feb. 1838, *G.W. Barclay 2058* (BM, MO, US); Corinto, 10 Nov. 1911, *A.S. Hitchcock 8743* (NY, US); Potosí, 1 Dec. 1973, *S.A. Marshall & D.A. Neill 6608* (NY); El Viejo, Reserva Natural de Consiguina, Comunidad La Salvia, 50 m, 13°00'N, 87°37'W, 28 Dec. 2006, *I. Coronado & R.M. Rueda 3566* (MO); **Chontales**. 2.8 km N of Cuapa, roadside, pastures, along a small stream, 21 Jan. 1978, *P.C. Vincelli 68* (MO); Hacienda Veracruz, including Cerro La Batea and Cerro Los Charcos, 120-475 m, 12°11'N, 85°21'W, 4-6 Aug. 1983, *W.D. Stevens 22424* (MO); **Estelí**. Reserva Cerro Tomabú, Comunidad Las Cuevas, 1000-1300 m, 13°01'N, 86°17'W, 24 Feb. 2000, *R. Rueda & al. 12891* (MO); Estelí, Miraflor, Moropotente, parcela 2 en la Comunidad El Coyolito en la propriedad del Sr. Alberto Rugama, 910 m, 13°12'43"N, 86°19'50"W, 23 Oct. 2007, *N.P. Rugama 26* (MO); Condega, Comunidad Venecia, 600-800 m, 13°24'60"N, 86°14'25"W, 24 Jan. 2008, *C.A. Padilla Gomez 195* (MO); **Granada**. Extinct Volcano Mombacho, 9 Jan. 1969, *D.A. Dudey & A.D. Moore 1948* (NY); Isla Zapatera, costado NE de Haciebda Santa Maria, 100 m, 11°45'05"N, 85°50'28"W, 22 Nov. 1982, *A. Grijalva 1870* (MO); Granada, Reserva Natural Mombacho, 1150-1350 m, 11°50'27"N, 85°58'59"W, 2 Dec. 2003, *R. Rueda & D. Paguaga 17662* (MO); **Jinotega**. Al NE de Wiwili, camino entre El Carmen y Wamblan, ca. 1 km al N del Carmen, 300-400 m, 13°43'N, 85°46'W, 2 Mar. 1980, *M. Araquistain & P.P. Moreno 1521* (MO); Wiwili, Comunidad de Inipuwas, Caño Wayawas, Transecto 8, Caceria (Limsitingni), 135 m, 14°23'N, 85°09'W, 10 Nov. 2005, *I. Coronado & al. 2568* (MO); Entre Yali y San Rafael del Norte, 936 m, 13°17'34"N, 86°11'09"W, 5 Sep. 2010, *I. Coronado & al. 5446* (MO); **León**. Quesalguague, 17 Jan. 1903, *C.F. Baker 2105* (G, K, MO, US, W); Isla Momotombito, NW slope, 40-300 m, 12°21'N, 8628'W, 11 Jun. 1979, *W.D. Stevens & al. 13237* (MO); Sauce, camino entre El Sauce y el empalme de Villa Nueva, 150 m, 12°55'N, 86°49'W, 10 Dec. 2006, *I. Coronado G. 3555* (MO); Salinas Grande, Isla Juan Venado, 12°18'N, 86°59'W, 2 Jan. 2009, *I. Coronado & R.M. Rueda 5053* (MO); **Managua**. Vicinity of Managua, 30 Jun. 1923, *W.R. Maxon & al. 7546* (US); Managua, Tipitapa, 31 Dec. 1969, *F.C. Seymour 2831* (BM, NY); 27 km S of Managua along Highway 8, 15 Jul. 1970, *G. Davidse & R.W. Pohl 2379* (K, L, MO, NY, US); Gallery forest long Río Santa Clara, near km 34.5 carretera a León, 150 m, 2 Nov. 1977, *D. Neill 2875* (M); Laguna de Apoyeque, 200 m, 12°15'N, 86°20'W, 10 Nov. 1989, *P.P. Moreno 27169* (MO); **Masaya**. 1-8 Nov. 1911, *A.S. Hitchcock 8710* (NY, US); Masaya, Lake Masaya, 11 Jan. 1970, *J.T. Atwood 3289* (BM, MO, NY); Parque Nacional Volcán Masaya, 250 m, 11°59'N, 86°07'W, 26 Aug. 1978, *D.A. Neill 4624* (MO); **Matagalpa**. Along Highway to Magatalpa, 29 Oct. 1968, *A. Molina 22858* (G, NY); **Nueva Segovia**. 3 km W of Ocotal, 20 Dec. 1968, *D.A. Dudey 778* (K); Nueva Segovia, 3 km W of Ocotal, 20 Dec. 1968, *F.C. Seymour 845* (BM, NY); **Rivas**. Rivas, Sapoa, 7 Jan. 1969, *R.B. Hamblett 1874* (BM, NY); Isla Omotepe, Volcán Maderas, Blague, Hacienda Magdalena, camino entre Balgue y la hacienda, 50-150 m, 11°29'N, 85°31'W, 30 Apr. 1984, *W. Robleto 62A* (MO).

PANAMA. **Chiriquí**. Burica Peninsula, Corotu, 6 km W from the airport of Puerto Armuelles, 60-100 m, 8°16'N, 82°54'W, 23 Feb. 1973, *P. Busey 574* (MO); **Coclé**. Aguadulce, 5 Dec. 191, *H. Pittier 4998* (US); Fort Clayton, 4 miles W Anton on Río Chico, 8 Dec. 1965, *J.D. Dwyer 2598* (MO); Roadside pasture 20 miles S of Nata, 13 Apr. 1970, *T.B. Croat 9642* (MO); Nata, low disturbed llnanos, 27 Dec. 1970, *S. McDaniel & E.L. Tyson 14732* (MO); Coletada alrededores de Aguadulce, 10 Nov. 1972, *N. Lezcano 26* (MO, PMA); Río "Las Mendozas" Penonomé, 6 Oct. 1974, *J. Henriquez 14* (MO, PMA); **Herrera**. 13 Sep. 1938, *P.H. Allen 797* (MO); Banks of Río Santa Maria, 23 Dec. 1966, *D. Burch & al. 1187* (MO); 5 km W of turnoff from Highway 105 to Potuga, roadside fields and pastures, 24 Oct. 1978, *B. Hammel 5275* (MO); Canazas, Divisa, 20 Apr. 1996, *N. Flores 71* (PMA); **Los Santos**. Monagre beach, 29 Jul. 1963, *J.D. Dwyer 4181* (BM, US); Las Tablas, 9 Aug. 1962, *J.D. Dwyer 2529* (US); Road between Tonosí and Guanaco, 28 Feb. 1963, *W.L. Stern & al. 1865* (MO, US); **Panamá**. Canal Zone, Chepo, Oct. 1911, *H. Pittier 4688* (BM, NY, US); Canal Zone, jungle along the shore, Taboga Island, 12 Sep. 1911, *A.S. Hitchcock 8068* (US); Canal Zone, in vicinity of Balboa, 9 Nov. 1911, *A.S. Hitchcock 8060* (US); Canal Zone, between Panamá and Corozal, 17 Dec. 1911, *A.S. Hitchcock 9204* (NY, US); Bella Vista, 29 Sep. 1912, *E.P. Killip 4040* (NY, US); Canal Zone, vicinity of Gatuncillo, 26 Feb. 1923, *C.V. Piper 5257* (US); Toboga Island, Dec. 1923, *P.C. Standley 27870* (US); Canal Zone, Balboa, Nov. 1923-Jan. 1924, *P.C. Standley 26077* (MO, US); Panamá, Punta Paitilla, 12 Jan. 1924, *P.C. Standley 30807* (US); Panamá, Toboga Island, 25 Jan 1935, *P.H. Allen 137* (G, MO, US); Trapicho Island, off coast of Pedro Gonzalez, Perlas Islands, 4 Jul. 1941, *P.H. Allen 2624* (MO, US); San José Island, Gulf of Panamá (about 55 miles SSE of Balboa); Panamá, Río Oharco-Espiritu on Tocumen Highway, 25 Sep. 1962, *J.A. Duke 5702* (MO); Canal Zone, Farfan Beach Area, 23 Oct. 1965, *E.L. Tyson 1806* (MO, USJ); San José Island, Perlas Archipelago, 1 Oct. 1945, *J. Harlow 73* (US); San José Island, Perlas Archipelago, 25 Jan. 1946, *I.M. Johnston 1255* (US); Canal Zone, Madden Dam, 10 Aug. 1960, *J.E. Ebinger 858* (MO, US); Paitilla, 26 Nov. 1960, *D. Sucre 123* (MO); Perlas Archipelago, Isla de La Bayonetia, 22 Aug. 1961, *J.D. Dwyer 1752* (US); Canal Zone, Fort Clayton, Los Santos, 16 mi S Macaracas at Quebrada Bejuco, 22 Jan. 1966, *E.L. Tyson & al. 3096* (SCZ); Chimán, 12 Dec. 1967, *W.H. Lewis & al. 3328* (MO, PMA); Saboga Island near village, Las Perlas Islands, 19 Dec. 1968, *E.L. Tyson 5150* (MO, US); Canal Zone, Los Santos, 5 mi S of Pocri, roadside near cultivated garden, 14 Apr. 1970, *T.B. Croat 9739* (MO, SCZ); Morro Island, just off N shore of Toboga Island, 25 Dec. 1974, *S. Mori & J. Kallunki 4075* (MO, PMA); Canal Zone, Fort Kobbe, Farfan area, 9 Nov. 1975, *W.G. D'Arcy 9619* (MO); Punta Chame, 10-15 miles from Pan American Highway, mangroves and savannas surrounding tropical dry forest, sea level, 17 Sep. 1981, *S. Knapp 1241* (MO); Cerro Ancon, 8 Oct. 1995, *B. Wong 71* (PMA); Amador, 1 Jul. 1995, *C. Guerra 394* (PMA); Carretera a Veracruz & instalaciones del Hospital de Palo Seco, 8°54'43"N, 79°33'51"W, 45 m, 27 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 907, 908, 909* (FT, PMA, SCZ); **Veraguas**. Puerto Mutis, 12 miles S of Santiago, 27 Dec. 1968, *E.L. Tyson 6028* (MO, US); Camino a Santa Fé, 27 Dec. 1971, *J. Cisneros 20* (MO, PMA); Llegando a la primera quebrada de Santiago, 28 Nov. 1985, *E. Rodriguez 64* (MO, PMA).

PERÚ. **Huachocolpa**. Quintabamba, 850-900 m, 21Apr. 1963, *O. Tovar 4141, 4144* (US); **Tumbes**. Cerros de Amotape, Quebrada Los Conejos and adjacent ridge, ca. 25 km SE of Cherrelique, 600-850 m, 04°09'S, 80°37'W, 10 Jun. 1987, *A. Gentry & C. Diaz 58299* (MO).

USA. **Florida**: Manatee Co. Tierra Ceia Island, 3 Oct. 1983, *J. Beckner 2633* (FTG).

VENEZUELA. **Anzotegui**. 21 km E of Piritu along Highway 9 to Barcelona, 15 m, 15 Dec. 1973, *G. Davidse 5020* (MO, US); Miranda, Boca del Pao, 08°03'20"N, 64°19'28"W, 20 Feb. 1985, *A. Castillo & A. Capobianco 1878* (MO); **Carabobo**. Hacienda Taborda, near El Palito, on the road from Valencia to Puerto Cabello, 0-200 m, 31 Dec. 1917, *H. Pittier 7686* (US); **Guárico**. 14 km N of Dos Caminos along Highway 2 to San Juan de Los Morros, 180 m, 12 Nov. 1971, *G. Davidse 3012* (MO), **n = 18!** (Davidse 1978); Aragua, 2.5 km directly S of Cata, 50 m, 15 Nov. 1971, *G. Davidse 3120, 3125* (MO); 15 km SW of Tamaco along carretera between Altagracia de Orituco and Chaguaramas, 150 m, 19 Nov. 1973, *G. Davidse 4220* (MO), **n = 18!** (Davidse 1978); Carretera Calabozo-San Fernando de Apure, 8°45'S, 67°32'W, 27 Jul. 1974, *G. Morillo & al. 4256* (NY); **Lara**. Palavecino, Hacienda Moron, 2 km fuera del caserio Quebrada Seca hacia Barquisimeto, carretera entre Broto y Acarigua, 19 Jul. 1978, *C. Burandt Jr. 298* (MO); **Táchira**. Middle slopes of Cerro El Rayo, between Aguas Calientes and La Rinconada, 550 m, 07°57'N, 72°25'W, 13 Nov. 1979, *J.A. Steyermark & al. 120268* (MO); **Zulia**. Vicinity of Mene Grande, 31 Oct. 1922, *H. Pittier 10617* (NY, US); Carretera El Consejo-Quiroz, 12 Oct. 1977, *G.S. Buntin 5685* (NY); Mara, alrededores de Campamento Carichuano (de Carbozulia), en la via entre el canho Paso de Diablo y el canho Vaqueta, 50-100 m, 10 Jul. 1981, *G.S. Bunting 10016* (MO, NY); Perirà, en km 38 de la carretera Machiques-La Fria, 22 Sep. 1982, *N. Galué 120* (NY).

(17) ***Lasiacis scabrior*** Hitchc., Proc. Biol. Soc. Wash. 40: 85. 1927. (Fig. 43).

Type: "*Guatemala, Alta Verapaz, Cubilqüitz, an Waldrandern, hoch klimmend, Februar 1913, H. von Tuerckheim 4036*" (holotype: US! [barcode US00134121]; isotype US! [barcode US00134120]).

Description

Perennials, robust caespitose. *Culms* 1-6(-8) m tall, erect at the base, arching and clambering upward over the vegetation, often rooting near the base; *internodes* up to 14 mm thick, hollow and lignified, papillose-pubescent toward the apex; *nodes* glabrous. *Leaf sheaths* usually pubescent to villous with hairs up to 2.0-3.0 mm long, overlapping margins ciliate with hairs 2.0-3.5 mm long; *collars* glabrous or slightly pubescent at the base; *ligules* 3.5-7.0 mm long, conspicuous, membranous, lacerate, glabrous to pubescent on the back side, margins ciliolate with hairs up to 3.0 mm long; *blades* 6.0-18 cm long, 1.3-3.0 cm wide, elliptic-lanceolate to linear-lanceolate, adaxial surface scabrid to the touch, puberulent along the midrib, abaxial surface densely puberulent, base asymmetrical, apex acuminate. Panicles 2.0-10 cm long, the base always included in the upper sheath, compact nearly spherical; *pedicels* divergent at maturity. *Spikelets* 3.5-4.5(-5.3) mm long, 2.8-3.5 mm wide, obovoid; *lower glumes* 1.5-2.8 mm long, 1.6-2.0 mm wide, 7-11-veined; *upper glumes* 3.8-4.8 mm long, 1.5-2.0 mm wide, 9-13-veined; *sterile florets* without a flowers, *lemmas* 11-13-veined, enrolling the palea at the margin**,** *paleas* ¾ to subequal to the length of the fertile floret; *fertile florets* 3.5-4.8 mm long, 1.6-2.0 mm wide, with an evident depression on the dorsal surface, *anthers* 2 mm long, white, *stigmas* white; *caryopses* 2 mm long, 1.5 mm wide. *Chromosome number*: unknown.

Iconographs

Fig. 100 (Davidse 2004).

Vernacular names

Belize: El Cayo, "*reed*", *P.H. Gentle 9023* (US); **Mexico**: "*carrizo*" and "*nángkuchip*" (Quattrocchi 2006).

Ethnobotanical and economic uses

Ecuador, "*used to feed guinea pigs*" (Bennet 1990).

Distribution

Belize, Brazil (Pará), Caribbean (Saba Island), Colombia, Costa Rica, Ecuador, Guatemala, Guyana, Honduras, Mexico, Nicaragua, Panama, Perú, Venezuela. (Fig. 44).

Distribution (bibliographic references)

Hitchcock (1930); Swallen (1931, 1943, 1955b); Standley (1937); Beetle (1977); Davidse (1978, 1994, 2001, 2004); Pohl (1980); D'Arcy (1987); Serna and López-Ferrari (2000); Morales (2003); Zuloaga et al. (2003); Correa et al. (2004); Renvoize et al. (2006); Davidse et al. (2007); Hokche et al. (2008); Sutherland (2008); Giraldo-Cañas (2011); Villaseñor (2016); Dávila et al. (2018); Sánchez-Ken (2019); Menjivar et al. (2021).

Ecology

Edges of wet forests, also in open areas along trails. From sea level up to 1000 ml.

Phenology

January through May. Late in the year September through December.

Remarks

Lasiacis scabrior is one of the most distinctive species in the genus. Culms erect, ligules up to 7 mm long,

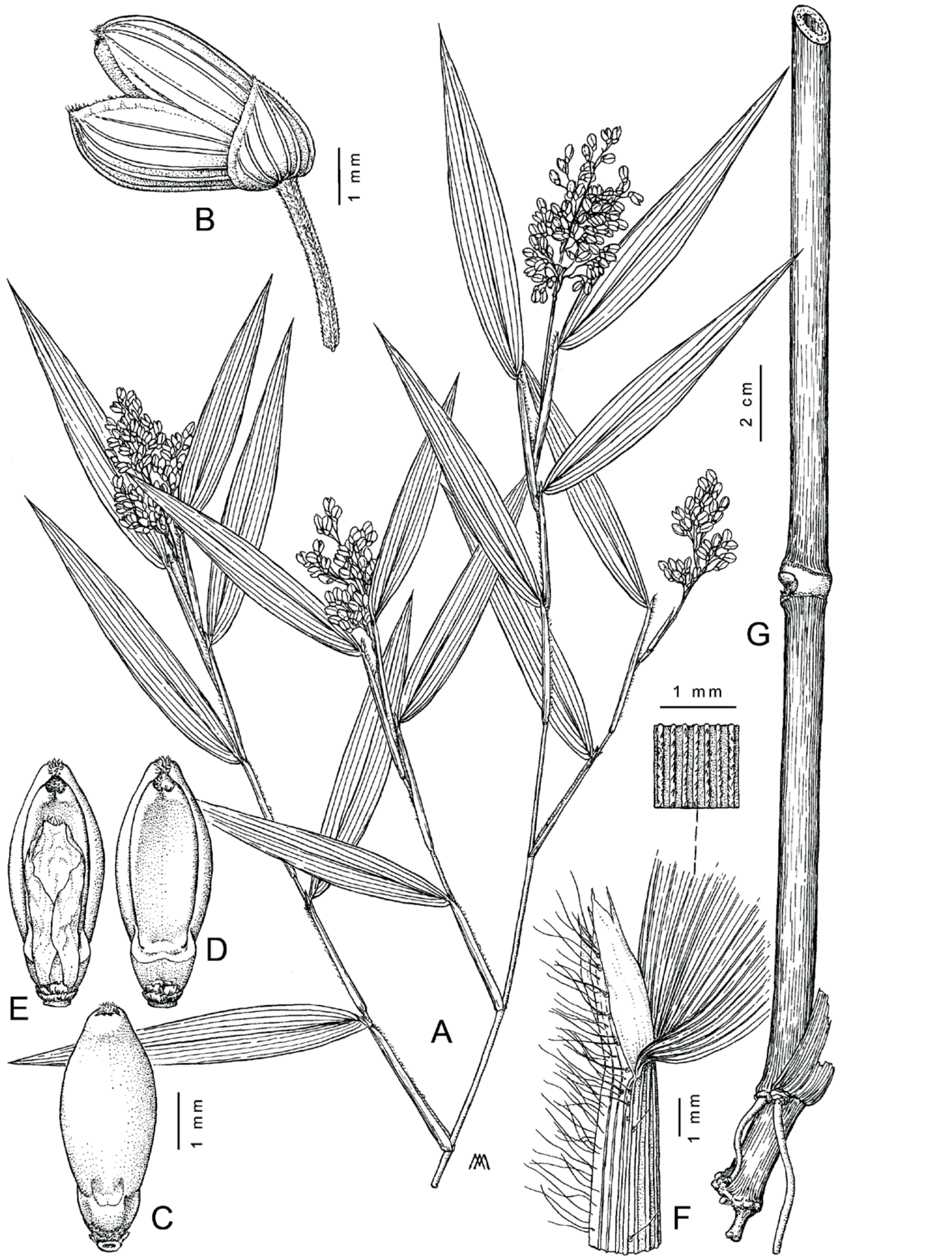

Figure 43. *Lasiacis scabrior* Hitchc.: **A**. Habit [A. from *A.F. Skutch 2155* (K)]; **B**. Spikelet lateral view; **C**. Fertile upper floret dorsal view; **D**. Fertile upper floret ventral view without lower persistent palea; **E**. Fertile upper floret ventral view with lower persistent palea; **F**. Ligular area; **G**. Culm at medium length with robust roots at the nodes [B-G. from *R.W. Pohl & G. Davidse 10791* (K)]. *A. Maury delineavit*.

Figure 44. *Lasiacis scabrior* Hitchc.: general geographic distribution.

with spherical panicles, mostly included in the upper sheaths. The upper leaf surface is very scabrid to the touch. Due to its long ligules, *L. scabrior* can be compared to *L. ligulata* and *L. standleyi* but differs in its panicle patterns. *Lasiacis scabrior* is mainly a Central American species occurring throughout West Indies to South America in Colombia, Venezuela, Ecuador, Peru, and northern Brazil (Parà). Perhaps this species is more common than originally thought and deserves more attention in the field, and in herbaria.

Selected specimens

BELIZE. **Cayo**. Hummingbird Highway, 13 Feb. 1956, *P.H. Gentle 9023* (US); **Cayo**. Track from Ceibo Chico to Ceibo Grande, 16°33'09"N, 89°06'38"W, 488 m, 10 Mar. 2000, *M. Short & al. 185* (PMA). **Toledo**. Between Rancho Chico and Cockscomb, Monkey River, 10 Apr. 1943, *P.H. Gentle 4398* (US); Sulphur Hill, Edwards Road beyond Columbia, 15 Jan. 1948, *P.H. Gentle 6366* (BM); Salomon Camp, vicinity of the junction of Richardson Creek and Bladen Branch, Mar. 1987, *G. Davidse 32159* (K); Southern Maya Mountains, Bladen Nature Reserve, trail from central Snake Creel Camp to Roochire Selipan archeological site, 450 m, 16°27'48"N, 88°58'42"W, 29 May 1997, *G. Davidse & H.B. Buchanan 36944* (MO).

BRAZIL. **Pará**. Boa Vista on the Tapajos River, May-Jun. 1929, *B.E. Dahlgren & E. Sella 198* (US).

COLOMBIA. **Chocó**. Near Ciudad Mutis, 75 m, 21-23 Feb 1939, *E.P. Killip & al. 33554* (US), *33594* (BM, US); Chocó, peak over R. Curundu, 1800 ft, 8 Mar. 1968, *J.A. Duke 15311* (MO); **Valle**. Cordillera Occidental, hoya del Río Digua, Quebrada del Río Blanco, 350 m, 18 Dec. 1942, *J. Cuatrecasas 13674* (MO, US).

COSTA RICA. **Alajuela**. Wet forest near Río San Rafael, 2 km W of La Marina, Llanura de San Carlos, 17 Feb. 1966, *A. Molina & al. 17385* (NY); About 8 km S of Colonia Blanca off a lumber road leading NE toward Volcán Santa Maria, 28 Feb. 1978, *F. Almeda 4021* (NY); Between Cerro Chado and Cerro de los Perdidos, 17 Feb. 1989, *G.F. Russell & al. 769* (US); **Cartago**. Turrialba, 5 Feb. 1965, *E.W. Lathrop 5522* (K); **Guanacaste**. La Tejon, N of Tilaran, 25 Jan. 1926, *P.C. Standley & J. Valerio 45897* (US); Parque Nacional Gunacaste Estación titilla, 600 m, 11°02'N, 85°.25 3'W, 24 May 1989, *B. Hammel 17386* (MO, USJ); **Heredia**. Finca La Selva, the OTS field station on the Río Puerto

Viejo just E of its junction with the Río Sarapioqui, 2 Apr. 1980, *B. Hammel 8404* (MO); Parque Nacional Rincon de la Vieja, the SE slopes of Volcán Santa Maria, above Estación Hacienda Santa Maria, 900-1200 m, 10°47'N, 85°18'W, 27-28 Jan. 1983, *G. Davidse et al. 23384* (MO); Finca La Selva, the OTS Field Station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí, 12 Jan. 1995, *R.L. Wilbur 63341* (USJ) 23 Jan. 1995, *R.L. Wilbur 63701* (MO, USJ); Finca La Selva, the OTS Field Station on the Río Puerto Viejo just E of its junction with the Río Sarapiqui, 100 m, 20 Feb. 1998, *R.L. Wilbur 70209* (PMA); **Limón**. Vicinity of Guapiles, 12-13 Mar. 1924, *P.C. Standley 37178* (US); Limón, main road beyond river from Rubber Station, Los Diamantes, 1 Mar. 1956, *B.G. Schubert 1137* (US); Limón, Canton de Talamanca, R.V.S. Gandoca-Manzanillo, Caribe Sur, 9°38'00"N, 82°38'26"W, 4 Mar. 1999, *U. Chavarria 1943* (MO); **Puntarenas**. Golfo Dulce and Río Térraba, Dec. 1947, *A.F. Skutch 5391* (US); Near Finca Las Crucis near San Vito de Java, 28 Jul. 1968, *R.W. Pohl & G. Davidse 10791* (K, US); 3 km NE of Quepos, 29 Jan. 1969, *R.W. Pohl & G. Davidse 11692* (K, US); Río Agua Buena near Airport, Rincon de Osa, 10 Feb. 1974, *R. Liesner 1988* (K, MO); Las Cruces, 1300 m, 11 Jan. 1978, *T.B. Croat 44409* (MO); Foothills of the Cordillera de Talamanca, vicinity of Helechales, along Río Guineal, 1100-1200 m, 9°04'30"N, 83°05'W, 29 Mar. 1984, *G. Davidse & G. Herrera 26272* (K, MO); Canton de Osa, camino a la toma de agua, Rancho Quemado Rincon, 200 m, 8°42'N, 83°34'W, 9 Dec. 1990, *Fco. Quesada 279* (BR, MO); Canton de Sierpe, high forest W of Rancho Quemada on road to Drake and new logging road, 1-300 m, 8°42'00"N, 83°36'00"W, 7 Feb. 1991, *P.J.M. Baas 7887* (MO); Canton Osa, Osa Peninsula, 24 Dec. 1992, *J.R. Grant & J.R. Rundell 2216* (US); Along edge of Zona Protectora Las Tablas near Las Alturas Biological Station, 1500 m, 10°10'N, 83°10'W, 1 Sep. 1995, *K. Holl 1050* (USJ); Canton de Golfito, P.N. Corcovado, Peninsula de Osa, Estación de Oro, Sendero El Acueducto, 180 m, 8°33'30"N, 83°30'10"W, 14 Mar. 1996, *L. Angulo 551* (MO); **San José**. Vicinity of El General, Dec. 1935, *A.F. Skutch 2155* (K, MO, NY, US); Vicinity of El General, Jan. 1939, *A.F. Skutch 3871* (K, MO, NY, US); El General Valley, vicinity of San Isidro, 28 Feb. 1966, *A. Molina & al. 18111* (BM); Pérez Zeledón, Páramo, Los Angeles, 23 Mar. 1998, *A. Estrada 1488* (K); Pérez Zeledón, Barú, 253 m, 9°25'50"N, 83°59'40"W, 6 Feb. 2001, *S. Lobo 218* (K, MO); **Talamanca**. Lisieré de la forét de Shiroes, Feb. 1895, *A. Tonduz 9213* (G, US); Talamanca, Apr. 1895, *H. Pittier 9492* (US, W).

ECUADOR. **Esmeraldas**. Esmeraldas Guadal, 20 may 1949, *M. Acosta Solís 12433* (US); Quininde Cantón, Bilsa Biological Station, Montañas de Mache, 35 km W of Quinindé, 5 km W of Santa Isabel, 400-600 m, 00°21'N, 79°44'W, 11 Nov. 1994, *M.S. Bass & al. 231* (BM, MO); Quinide canton, The Mache-Chindul Ecological Reserve, Bilsa Biological Station, Mache Mts. 35 km W of Quinindé, 500 m, 00°21'N, 79°44'W, 4 Dec. 1996, *J.L. Clark & al. 3557* (MO, US); **Guayas**. Teresita, 3 km W of Bucay, 270 m, 5-7 Jul. 1923, *A.S. Hitchcock 20438* (NY, US); **Manabí**. Manabí, 29 Nov. 1939, *O.L. Haught 2973* (US); Jama, Cordillera de Jama, coastal range, 12 km E of Jama, 300 m, 00°15'S, 80°13'W, 16 Dec. 1998, *D. Neill & al. 11562* (MO); **Morona-Santiago**. Río Yunganza, Road Límon-Méndez, 23 Sep. 1979, *L. Holm-Nielsen & al. 20385* (K); Centro Shuar Yukutais, East side of Río Yukutais, 950-1020 m, 03°30'S, 78°10'W, 6 Nov. 1988, *B. Bennett 3527* (MO, NY); Canton, Macas, Bosque Protector Do Mono, 1170 m, 02°13'38"S, 078°07'23"W, 15 Aug. 2005, *J.L. Clark 9339* (NY, US); **Napo**. Orellana Canton, Parque Nacional Yasuni, Carretera y oleoducto de Maxus en construccion, 240 m, 03°05'S, 76°29'W, 29-31 May 1994, *A. Dik 1388* (MO); **Pastaza**. Canton, Pozo Petroliero "Corrientes" de Unocal, 300 m, 76°49'W, 01°43'S, 1-31 Aug. 1990, *E. Gudiño 531* (MO, US); **Pichinca**. Shinguipino, between Ríos Napo and Tena 8 km SE of Tena, Cerro Antisana, rain forest, 30 Aug. 1960, *P.J. Grubb & al. 1521* (K, NY); 20 km W of Santo Domingo de los Colorado, banks on the river Huacuhua, 1000 ft, 23 Oct. 1961, *P.C.D. Cazalet & T.D. Pennigton 5125* (K, NY, US); S.to Domingo de los Colorados, 28 Nov. 1952, *F. Fagerlind & G. Wibom 1594* (MO, UPS); Km 127 on road Quito-Puerto Quito, 500 m, 00°06'N, 79°09'W, 14 Jul. 1985, *S. Lægaard 54629* (K, MO); **Santiago-Zamora**. Cordillera Cutucu, 2800 ft, 2°40'S, 78°W, 17 Nov.-5 Dec. 1944, *H. Jorgenson 1119* (NY, US).

GUATEMALA. **Alta Verapaz**. Sebol, 13 Apr. 1964, *E. Contreras 4270* (US); **Petén**. Lacandon, about 3 km NW on trail to Tenosique, 6 Feb. 1962, *E. Contreras 3327* (US); Guayacan, on al Camino al Ceibo, 3 km, 10 Jan. 1968, *E. Contreras 7425* (NY); Los Arcos, on Cadenas Road, 21 Dec. 1969, *E. Contreras 9437* (NY); La Cumbre, on km 138 bordering Cadenas Road, 13 Feb. 1971, *E. Contreras 10492* (NY); Petén, en el camino para San Luis, 7 Jan. 1972, *R.T. Ortíz 2171* (US).

GUYANA. **Rupununi**. Basin of Rupununi River, Isherton, 9-15 Nov. 1937, *H.H. Smith 2417* (G).

HONDURAS. **Atlantida**. 28 km NE of El Progreso, 150 m, 24 Jun. 1970, *G. Davidse & R.W. Pohl 2173* (MO, US); **Gracias a Dios**. Río Patuca, 0-200 m, 1994-1995, *P. House 1238* (BM, BR, MO); **Olancho**. Carretera entre Catacamas y Juticalpa, orillas del riachuelo Aguaquire, 700 m, 1-4 May 1975, *C. Nelson & E. Vargas 2719* (MO); Olancho, Río Incendio, 5 Mar. 1982, *S. Blackmore & G.L.A. Heath 2145* (BM, MO); **Yoro**. Cordillera Nombre de Dios, between Río Guán Guán and Quebrada Aguatacal, 4 Mar. 1993, *R. Evans 1315* (BM, US).

MEXICO. **Chiapas**. Ocosingo, tropical rain forest, at the ruins of Yaxchilan on the banks of the Río Usumacinta, 26 Feb. 1973, *D.E. Breedlove 33955* (NY); Las Margaritas, tropical rain forest, low ridges at the confluente of the Río Ixcàn with the Río Lacantum (Río Jatatè) on the Guatemala border, 14 Mar. 1973, D.*E. Breedlove & E. McClintock 34090* (NY); Ocosingo, 5 km SW of Santo Domingo, 13 May 1982, *G. Davidse & al. 20420* (BM); **Oaxaca**. 7 Mar. 1978, *A. Delgado & al. 950* (L); Uxpanapa Region, along gravel road between Esmeralda and Río Verde, 17°10'N, 94°45'W, 19 Jan. 1987, *T.B. Croat & D.P. Hannon 63308* (K, US); **Veracruz**. Fortuño, Coatzacoalcos River, 1937, *L.O. Williams 8615, 8960* (G, P, US, W); Veracruz, Hidalgotitlan, 21 Mar. 1973, *A. Juan 13* (BM).

NICARAGUA. **Atlantico Norte**. Musawas, Reserva Bosawas, Musawas, 50-150 m, 14°14'00"N, 84°43'00"W, 3 Mar. 2001, *C. Aker 449* (MO); **Carazo**. Bluefields, summit and slopes of Cerro San Isidro, 28 Mar. 1966, *G.R. Proctor & al. 27281* (MO, NY, SD, US); Granada. Volcán Mombacho, 20 Feb. 1903, *C.F. Baker 2454* (G, K, L, MO, US, W); **Jinotega**. Wiwili, Reserva de Bosawas, Cominidad Inipuas, Transecto 3, ubicado en zona agricola, 185 m, 14°24'32"N, 85°11'06"W, 16 Apr. 2005, *I. Coronado & al. 1584* (MO), *1594* (P); Wiwili, Comunidad La Esperanza Reserva Bosawas, Territorio Miskito Indian Tasbaika Kum, parcela 2 en el Tacotal, 500 m al oeste de la Finca de Lionidas, 60-70 m, 4 Mar. 2008, *D. Prado G. 276* (MO); **Río San Juan**. El Castillo, Sabalos, comarca Las Maravillas, 11°08'N, 84°39'W, 14 Jan. 1995, *R. Rueda & al. 2745* (MO); El Castillo, Comunidad Aguas Zarcas, 2 km al norte del puesto de guardaparques, 350 m, 11°14'22"N, 84°14'16"W, 12 Mar. 2005, *A. Urbina 181* (MO); **Zelaya**. Ca. 6.3 km S of bridge at Colonia Yolaina and ca. 0.8 km S of ridge of Serranias de Yolaina on road to Colonia Manantiales (Colonia Somoza), 200-300 m, 11°36'N, 84°22'W, 13-14 Feb. 1978, *W.D. Ste-*

vens & al. 6390 (MO); Zelaya, ca. 13 km above Kururia, 200 m, 14°39'N, 84°04'W, 2 Mar. 1979, *J.J. Pipoly 3786* (BM, MO); Zelaya, Alrededores del poblado Nueva Atlanta, 11°34'N, 84°26'W, 19 Feb. 1994, *R. Rueda & al. 3246* (MO).

PANAMA. **Bocas del Toro**. SE y NE del campamento Changuinola 1 del IRHE, 19 Jan. 1980, *M.D. Correa & al. 3351* (MO, NY, PMA), *3388* (MO); Isla San Cristobal, 2 km W of Bocatorito, 60 m, 8 Feb. 1989, *P.M. Peterson & C.R. Annable 6711* (MO); Approximately 3 km S of Tiger Key, 0-30 m, 25 Feb. 1989, *P.M. Peterson & C.R. Annable, 7102, 7110* (MO); Camino a Quebrada Rabo de Puerco, 9 Mar. 1994, *Santamaría 761* (MA, PMA); Caribbean slopes of Cerro Fabrega at foot of "Falso Fabrega" in Palo Seco Reserve, second northernmost tributary (on map) of Culubre river; Río Liso Camp, 840 m, 09°09'N, 82° 40'69W, 16 Mar. 2005, *A.K. Monro & S. Cafferty 4661* (MO, PMA); Changuinola, Bosque Protector Palo Seco, Charco La Pava, Comunidad de Guayacán, 9°09'31"N, 82°30'35"W, 424 m, 4 Feb. 2014, *O.O. Ortiz & R.M. Baldini 2105* (FT, PMA); **Chiriquí**. Burica Peninsula, San Bartolo Limite near Costa Rican border, 12 miles W of Puerto Armuelles, 400-500 m, 24 Feb. 1973, *T.B. Croat 22169* (MO, US); 1 mile E of Cañas Gordas, near Costa Rica Border on road to volcano, 800-1200 m, 26 Feb. 1973, *R. Liesner 267A* (K, MO); 19 km W of Río Chiriquí Viejo on road to San Sereno, 1000-2000 m, 17 Mar. 1977, *W.G. D'Arcy 10838* (PMA, MO, US); **Coclé**. N rim of El Valle de Antón, 600-1000 m, 12 Feb. 1939, *P.H. Allen 1641* (MO, NY); Coclé, vicinity of La Mesa, N of El Valle de Antón, 12 May 1941, *P.H. Allen 2376* (US); 4 miles W Antón on Río Chico, 10' tall in shade, 8 Dec. 1965, *E.L. Tyson & K.E. Blum 2598* (SCZ); Cerro Pilón, hill below summit, above El Valle de Antón, 2000-2700 ft, 28 Mar. 1969, *J.D. Dwyer & al. 4549* (MO); Hills above El Valle, 1000 m, 24 Dec. 1972, *A. Gentry 6897* (K, MO, PMA, US); 44 km N of Penononé on road to Coclesito, 300-500 ft, 21 Feb. 1978, *B. Hammel 1672* (MO); Above La Pintada, peak to E of Llano Grande-Toabré Highway, 1400-1900 ft, 15 Feb. 1981, *W.G. D'Arcy & K. Systma 14705* (MO); Coclé, Caribbean side of divide at El Copé, 200-400 m, 8°45'N, 80°35'W, 4 Feb. 1983, *C. Hamilton & G. Davidse 2736* (MO); **Colón**. Santa Rita Ridge, 500 m, 09°20'04"N, 79°45'04"W, 11 Jan. 1987, *G. MacPherson 10246* (MO, PMA); **Darién**. Vicinity of Campamento Buena Vista, Río Chucunaque above confluente with Río Tuquesa, 5 Jul. 1959, *W.L. Stern & al. 851* (G, MO); Agua Fria, ca. 8 miles N of Santa Fé, 50 m, 13 Feb. 1967, *J.A. Duke 10098(3)* (MO); Darién, Mannene to the mouth of the Río Coasi, 28 Apr. 1968, J.*H. Kirkbride & N. Bristan 1553* (MO, NY); W side of SW ridge leading to Alturas de Nique, headwaters of Río Coasi, 450 m, 27 Dec. 1980, *R.L. Hartman 12275* (MO); Río Cocalito, 17 Sep. 1982, *C. Whitefoord & A. Eddy 214* (BM, F, MO, PMA); Ensenada del Guayabo, 18 km SE of Jaqué, 50 m, 12 Jan. 1983, *N. Garwood & al. 185* (BM, MO, PMA); S of El Real on trail to Cerro Pirre, ca. 50 m, 8°00'N, 77°45'W, 27 Mar. 1985, *G. McPherson 6981* (PMA, US), *6987* (BM, K, MO, NY); **Panamá**. San José Island, Perlas Arch., about 55 mi. SSE of Balboa, 24 Mar. 1945, *I.M. Johnston 548* (BM, MO, US); Cerro Campana, 8 Jul. 1960, *J.E. Ebinger 340* (MO, US); Canal Zone, Fort Clayton, Los Santos, 11 mi N Tonasi, fruits black, very dense in woods, 23 Jan. 1966, *J. Dwyer 2977* (MO, SCZ); Cerro Jefe in "*Clusia*" forest, 2700-3000 feet, 27 Jan. 1966, *E.L. Tyson & al. 3327* (MO, SCZ); Tributary of Río Chagres, 5 miles SW of Cerro Brewster, 1000 ft, 14 Dec. 1967, *W.H. Lewis & al. 3376* (MO); Cerro Azul, 6-10 km del Lago Goofy, 700 m, 11 Mar. 1968, *C.E. Calderón 2091* (MO, US); Cerro Campana, above Su Lin Motel, rain forest, 25 Mar. 1969, *D.M. Porter & al. 4271* (MO); Slopes of Cerro Campana, 2700 ft, 23 Jan. 1970, *R.L. Wilbur & R.E. Weaver 11289* (MO, US); Panamá, near top of Cerro Jefe, 1 Jan. 1971, *A. Gentry 3511* (PMA); Canal Zone, Pipeline Road 12 miles from Gamboa Gate, 5 Mar. 1971, *T.B. Croat 13950* (MO); Cerro Jefe, 2900 ft, 1 Jan. 1972, *A. Gentry & al. 3514* (MO); 6-10 km N of Pan-American Highway on El Llano-Cartí Road, 9°15'N, 78°59'W, 200-250 m, 1 Apr. 1988, *S.A. Thompson 4690* (MO, PMA, US); **Los Santos**. Azuero Peninsula, along trail between Jobero and headwaters of Río Pedregal, 300-700 m, 28 Apr. 1976, *T.B. Croat 74* (MO); Los Santos, road to El Corteo, 100-200 m, 24 Jan. 1981, *W.G. D'Arcy & K.J. Sytsma 14348* (BM, MO); **San Blas**. El Llano-Cartí Road, 350 m, 9°19'N, 78°55'W, 2 Jan. 1985, *G. De Nevers & G. Herrera 4441* (K, MO, PMA); **Veraguas**. Veraguas, 6-7 km W of Santa Fe, 2900 ft, 16 Feb. 1974, *M. Nee 9778* (K, MO, PMA); NW of Santa Fé, 26 Feb. 1975, *S. Mori & J. Kallunki 4881* (K, MO, US); Veraguas, along steep trail to summit of Cerro Tute ca. 3 km above Escuela Agricultura Alto Piedra near Santa Fé, 3000-3100 ft, 4 Jan. 1981, *K. Systma & T. Antonio 3055* (MO).

PERÚ. **Huanuco**. Vicinity of Tingo Maria, Cordillera Azul, dense forest E of Koenig's along small stream to N of road, 22 Jun. 1959, *M.E. Mathias & D. Taylor 3463* (MO, US); **La Mar**. Ayachuco, 585 m, 12°23'N, 73°47'W, 8 Jun. 1968, *T.R. Dudley 10025* (MO); **Loreto**. Province C. Portello, Inchua, 4 Aug. 1946, *J. Soukup 3022* (US); Puranchim, Río Sinchiyacu, 200 m, 02°50'S, 76°55'W, 21-27 Nov. 1986, *W.H. Lewis & M. Elvin-Lewis 12106* (MO); **Madre de Dios**. Prov. Tambopata, Las Piedras, Cusco Amazónico, 200 m, 12°29'S, 69°03'W, 21 Jul. 1991, *M. Timaná 1907* (MO); **San Martín**. Lamas, Along Río Curiyacu, an affluent of Río Cumbasa, about 8 km above San Antonio, 7 Nov. 1937, *C.M. Belshaw 3615* (MO, NY).

VENEZUELA. **Amazonas**. Alto Orinoco, Raudal de los Guaharibos, 22 Jul. 1951, *L. Croizat 250* (NY).

VIRGIN ISLANDS. **Saba**. (Netherlands Antilles), first 500 meters of Sandy Cruz Trail entering from east end, disturbed area with cultivated plants, forming clump with arching culms, fruits black, 17°37'55"N, 17°38'08"N, 63°14'45"W, 63°14'52"W, 5 Mar. 2007, *S.A. Mori & al. 26723* (NY) .

(18) *Lasiacis sloanei* (Griseb.) Hitchc., Bot. Gaz. (Crawfordsville) 57: 302. 1911. (Fig. 45, 46).

Bas.: *Panicum sloanei* Griseb., Fl. Brit. W. Ind. 551. 1864.

Type: "*Jamaica, Manchester, woods near Broken(horn?), Nov. 1843, Purdie s.n.* (lectotype, designated by Davidse 1978: K! [barcode K000308121]; isolectotype: US! Fragment from K [barcode US00140000]).

(=) *Panicum latifolium* Ham., Prodr. Pl. Ind. Occ. 10. 1825, non L. (1753).

Type: "*Antilles, (ex spec. Hort. Paris)*" (Hamilton 1825: 10), "*Panicum latifolium*, *Le Calumet*", "*ex horto Reg*" (holotype: P! [barcode P00667321]).

(-) *Panicum divaricatum* J.Presl ex Griseb., Fl. Brit. W. Ind. 551. 1864, non L. (1759) *nom. inval.* [cited as a synonym of *P. sloanei* Griseb. (Grisebach 1864).

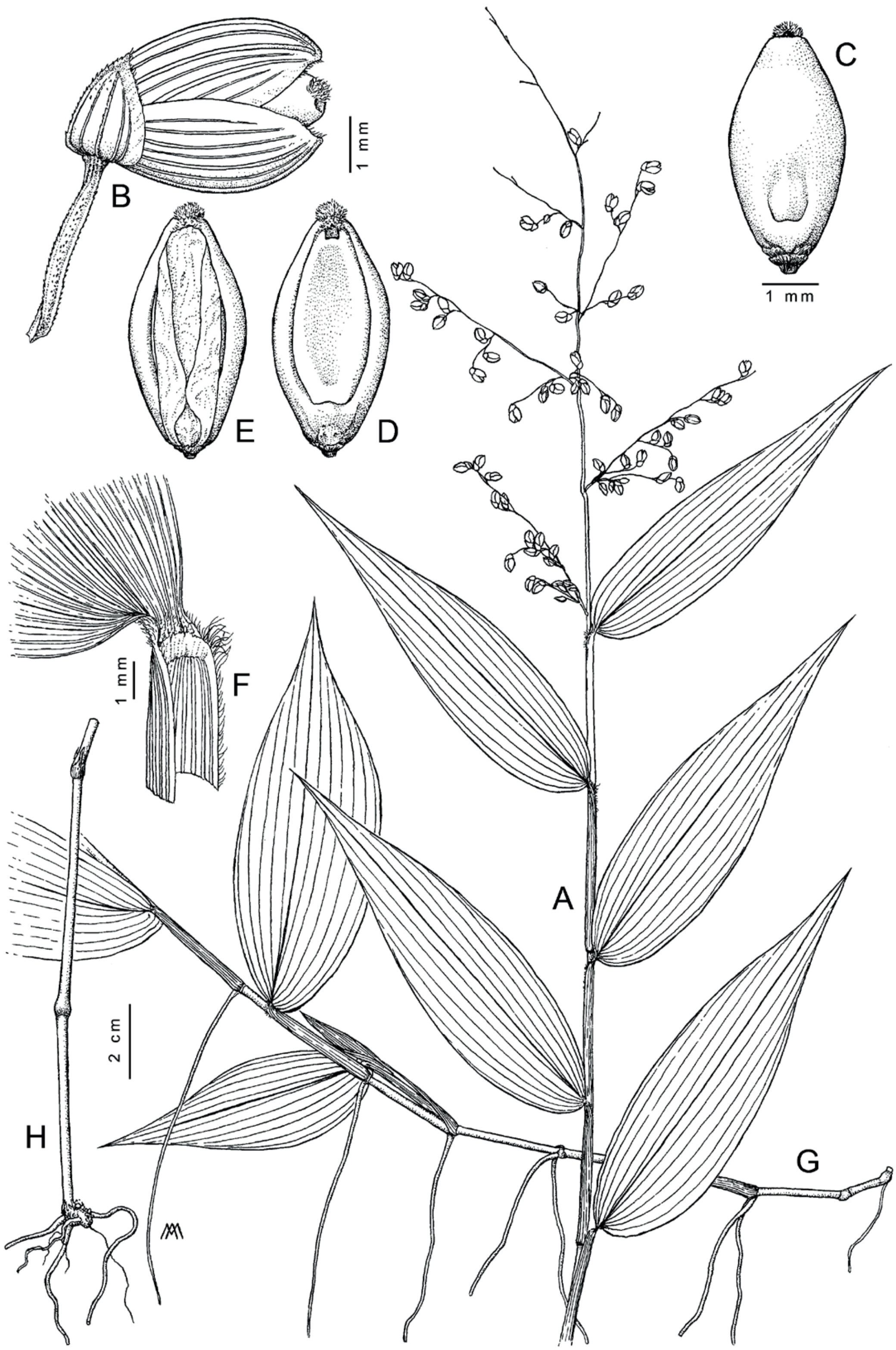

Figure 45. *Lasiacis sloanei* (Griseb.) Hitchc.: **A**. Habit [A. from *E.L. Ekman 12094* (K)]; **B.** Spikelet lateral view; **C**. Fertile upper floret dorsal view; **D**. Fertile upper floret ventral view without lower persistent palea; **E**. Fertile upper floret ventral view with lower persistent palea [B-E. from *R.W. Pohl & G. Davidse 10994* (K)]; **F**. Ligular area [F. from *A.S. Hitchcock 591* (K)]; **G**. Culm at medium length rooting at the nodes; H. Culm at the base [G-H. from *R.W. Pohl & G. Davidse 11123* (K)]. *A. Maury delineavit.*

Figure 46. *Lasiacis sloanei* (Griseb.) Hitchc.: habit. (Panama, Cerro Campana, photo R.M. Baldini).

Description

*Perennials***,** caespitose. *Culms* 1–8 m long; erect, clambering and climbing into the vegetation; *internodes* 5–10 mm thick at maturity, hollow, usually glabrous. *Leaf sheaths* glabrous, ciliolate upward, auricular hairs 1.5–3.0 mm long; *collars* extended, forming a pseudopetiole up to 3–4 mm long, puberulent to short-hispid; *ligules* 0.5–1.0 mm long, membranous, inconspicuous, ciliolate with small hairs up to 0.5 mm long, puberulent on the back side; *blades* 8–20 cm long, 1.5–5.0 cm wide, ovate to ovate-lanceolate, adaxial surface puberulent or slightly scabrous, adaxial surface glabrous, base asymmetrical, apex acuminate, margins scabrid. *Panicles* 5–38 cm long, open, with few short-pedicelled spikelets; *upper branches* ascending to widely spreading, scabrid. *Spikelets* 4.0–5.5 mm long, 2.8–3.5 mm wide; *lower glumes* 1.5–2.5 mm long, 0.8–1.5 mm wide, 7–9-veined; *upper glumes* 3.8–5.0 mm long, 1.7–2.0 mm wide, 9–13-veined; *sterile florets* often staminate or rudimentary, *lemmas* 9–13-veined, *paleas* ¾ to equal the length of the fertile floret; *fertile florets* 3.8–4.8(–5.0) mm long, 2.3–2.8 mm wide, *anthers* 1.6–2.0 mm long, white, *stigmas* white; *caryopses* 2.3–2.7 mm long, 2.0 mm wide. *Chromosome number*: $2n = 36$ (Reeder 1968); $n = 18$ (Davidse 1972, 1978).

Iconographs

Fig. 99 (Davidse 2004); Lámina 157 (Catasús Guerra 2012b).

Vernacular names

Cuba: "*canutillo*" (Catasús Guerra 2012a), "*canutillo cimarrón*", "*tibisi*" (Acevedo-Rodríguez and Strong 2012); **Dominican Republic**: "*calimete*" Acevedo-Rodríguez and Strong 2012); **Guatemala**: Petén, "*carrizo*" *E. Contreras 1846* (US); **Haiti**: "*calumete*", "*calumette*" (Acevedo-Rodríguez and Strong 2012); **Honduras**: Copán, "*carrizo*" *A. Molina & Albertina R. 34261* (US); **Mexico**: "*otate*" (Quattrocchi 2006).

Distribution

Belize, Bolivia, Colombia, Costa Rica, Cuba, Ecuador, El Salvador, Haiti, Dominican Republic, Guatemala, Honduras, Jamaica, Leeward Islands (Antigua, St. Martin), Mexico, Nicaragua, Panama, Puerto Rico, Suriname, Venezuela. (Fig. 47).

Distribution (bibliographic references)

Hitchcock and Chase (1917); Hitchcock (1911, 1920, 1930); Urban (1921); Swallen (1931, 1934, 1936, 1955b); Standley (1937); Pinto-Escobar (1966); Adams (1972); Beetle (1977); Howard (1979); Davidse (1978, 1994, 2001, 2004); Pohl (1980); Serna and López-Ferrari 2000); Morales (2003); Zuloaga et al. (2003); Renvoize et al. (2006); Davidse et al. (2007); Hokche et al. (2008); Sutherland (2008); Giraldo-Cañas (2011); Acevedo-Rodríguez and Strong (2012); Catasús-Guerra (2012a); Villaseñor (2016); Dávila et al. (2018); Sánchez-Ken (2019); Menjivar et al. (2021).

Ecology

Edges of wet montane forests, also at montane roadsides. From sea level to 1780 m [El Salvador: Santa Ana, 1780 m *J. Monterosa 918* (MO)] and 1900 m [Colombia: Santander, *E.P. Killip & A.C. Smith 19411* (US)].

Phenology

July through April.

Remarks

Lasiacis sloanei is a very distinct species with culms up to 6 m tall, erect to clambering, rooting at the nodes, ovate to ovate-lanceolate, up to 20 cm long and 5 cm wide, glabrous leaf blades [*E.L. Ekman 15851* (G, US)],

Figure 47. *Lasiacis sloanei* (Griseb.) Hitchc.: general geographic distribution.

glabrous, long open panicle. Its distribution is centered in Central America and Caribbean, scattered in South America (Colombia, Venezuela, Suriname, and Ecuador).

Selected specimens

BELIZE. **Cayo**. Hummingbird Highway, 12 Dec. 1955, *P.H. Gentle 8980* (BM, NY, US); Central Farm, Sep. 1964, *R.H.L. Disney A380/D* (BM); SW of Cayo on road to Benque Viejo, 29 Nov. 1968, *R.R. Innes 74* (K); W of Hummingbird Highway at a point 7 miles S of its junction with Western Highway, N boundary of Roaring River Est, 80 m, 13 Jul. 1970, *D.L. Spellman & W.W. Newey 1661* (MO); 3 mi. S of Guacomallo bridge, 28 Aug. 1980, *D. Sutton & al. 299* (BM, MO); 10 miles from San Ignacio, Chaa Creek Road, IxChel Farm, 17°61'N, 89°4'W, 15 Aug. 1987, *R. Arvigo 48* (MO, US); **Orange Walk**. Honey Camp, Oct. 1929, *C.L. Lundell 555* (K, MO, NY, UPS, US); **Toledo**. Cero, 1 Feb. 1950, *P.H. Gentle 6966* (US); Gracie Rock, 4-5 Jun. 1973, *T.B. Croat 23912* (K, L, MO, NY); Las Sierritas, 20 km W of Big Creek Settlement, eastern slope of Cerrito, the tallest hill in Las Sierritas range, 80-120 m, 16°31'55"N, 88°35'48"W, 4 Dec. 1997, *T. Hawkins 1644* (MO).

BOLIVIA. **La Paz**. Sud Yungas, Alto Beni, Concesión de San José de Popoy, 580 m, 21 Oct. 1987, *R. Seidel & E. Vargas 2155* (US).

COLOMBIA. **Magdalena**. Santa Marta, 1898-1901, *H.H. Smith 2145* (BM, G, K, L, MO, NY, P, US); In forest long indian trail to Pueblito, Parque Nacional Tayrona, 50 m, 11°19'N, 73°58'W, 24 Oct. 1972, *J.H. Kirkbride 2496* (MO, NY, US); **Meta**. Río Güejar about 10 km below junction with Río Zanza, north end of Cordillera Macarena, 470 m, 21 Aug. 1950, *S.G. Smith & J.M. Idrobo 1534* (K, MO, NY, US); **Risaralda**. Pereira, Hacienda Corsega, a 18 km de La Virginia por carretera, a 7 km al W de carretera La Virginia-Cerritos por carretera a El Trapiche, 900 m, 12 Feb. 1990, *P.A. Silverstone-Sopkin & al. 5913* (MO); **Santander**. Between El Roble and Tona, 1500-1900 m, 17 Feb 1927, *E.P. Killip & A.C. Smith 19411* (US); Río Caquetá, 18 Oct. 1990, *van Dolmen & Matapi 20* (K).

COSTA RICA. **Cartago**. Turrialba, Instituto Interamericano de Ciencias Agrícolas, Canyon of the Río Reventazón, 602 m, 14 Aug. 1966, *R.W. Pohl & C. Calderón 10300* (MO); Canyon of Río Reventazón, near Turrialba, 6 Aug. 1968, *R.W. Pohl & G. Davidse 10832* (K, US); Canton de Turrialba, Cordillera de Talamanca, along W side of Río Chirripó from Quebrada Bolori to

Quebrada Kulri, 575-625 m, 9°46'30"N, 83°23'30"W, 8 Aug. 1995, *M. Grayum 10813* (MO); **Guanacaste**. Upala Road, ca. 30 km N of Cañas, forested area along Río Chiquito, 400 m, 25 Jul. 1971, *R.W. Pohl 12637* (MO), **n = 18**! (Davidse 1978); **Limón**. Along Río Estrella, near Pandora, 19 Sep. 1968, *R.W. Pohl & G. Davidse 11123* (K, US); **Puntarenas**. N of the Carretera Interamericana along road to Boruca, 220 m, 22 Aug. 1968, *R.W. Pohl & G. Davidse 10994* (US), **n = 18!** (Davidse 1978).

CUBA. Cuba, s.d., *Ramon de la Sagra 44* (FI-Webb, G); Cuba, 1849, *F. Rugel 868*, *872* (BM, L, NY); s.l., 1865, *C. Wright 51* (K), *97* (K), *3878* (K, NY, P, US, W); **Cienfuegos**. Vicinity of Soledad, Aug. 1941, *R.A. Howard 6250* (NY, US); **Habana**. La Habana, Loma Esperón, 4 May 1914, *E.L. Ekman 653* (K); Pinar del Río, Mogote in front of La Güira S. Diego de Los Baños, 5 Jul. 1915, *Bro. León 5148* (US); Habana, Managua, 15 Feb. 1956, *C.V. Morton 10194* (US); **Mantanzas**. Mantanzas, 9 Sep. 1903, *N.L. Britton & P. Wilson 393* (NY); On limestone, near Boca de Canasí, 7 Dec. 1927, *Bro. León 13171* (US); **Mayabeque**. Vicinity of Madruga, 28 Mar. 1903, *N.L. Britton & al. 759* (NY); **Nueva Gerona**. Isle of Pines, near Nueva Gerona, 4 Jul. 1900, *W. Palmer & J.H. Ridley 1001* (NY); Isles of Pines, Sierra de Los Caballos, 2 Mar. 1916, *N.L. Britton & P. Wilson 15134* (US); **Oriente**. Mayarì arriba, at Río Mayarì, 7 Dec. 1922, *E.L. Ekman 15851* (G, US); **Pinar del Río**. 26 Jan. 1905, *C.F. Baker 4587* (W); Sierra Anafé, 19 Dec. 1911, *P. Wilson 11421* (NY, US); Sierra Mendoza, 25 Dec. 1911, *J.A. Shafer 11147* (NY, US); Sierra de Anafé, Loma San Gabriel, 21 Mar. 1920, *E.L. Ekman 10557* (NY); San Cristobal, Pinar del Río, Loma del Pimento, in thickets on the top of the mountain, 29 Nov. 1920, *E.L. Ekman 11528* (K); Las Pozas, in hills towards Pan de Guajaibon, 7 Jan. 1921, *E.L. Ekman 12743* (US); Mariel, 4 Jun. 1921, *E.L. Ekman 12853* (NY, US); Sierra de Anafé, Loma de San Gabriel near Guanajay, 11 Jul. 1921, *E.L. Ekman 13035* (G, US); Camagüey, Palo Seco, in forest at foot of Poma Decada, 3 Oct. 1922, *E.L. Ekman 15319* (US); Santa Cruz to Rangel, Sierra de Los Organos, 17-19 Nov. 1941, *C.V. Morton 4441* (US); **Santiago**. SE Villa Estate, near Santiago, 10 Sep. 1906, *N. Taylor 328* (NY); **Villa Clara**. Santa Clara, Cienfuegos, Cieneguita, 7 Feb. 1895, *R. Combs 55* (K, NY, P); Santa Clara, Limones, Soledad, Cienfuegos, 29 Jul. 1927, *J.G. Jack 5187* (NY, UPS, US).

DOMINICAN REPUBLIC. **Barahona**. El Firme, Cabral, 18 Aug. 1959, *J. de Jesus Jimenéz 3751* (US); **El Seybo**. Llano Costero, La Romana, near S. Pedro de Macorís, 6 Apr. 1929, *E.L. Ekman 12094* (K, NY, US); **San Pedro de Macorís**. Macoris, 23 km W of San Pedro de Macorís, 18 Oct. 1946, *R.A. Howard & E.S. Howard 9508* (NY, US); **Santiago**. Jaiquí Picado, 20 miles W of Santiago, 27 Nov. 1969, *A.H. Liogier 17049* (NY).

ECUADOR. **Esmeraldas**. Near Punta Galera at finca of Robin Gracia Montalvo, along watercourse in secondary rain forest, 0°48'N, 80°2'W, 30 m, 15 May 1988, *S. Lægaard & E. Kullberg 71243, 71248* (G).

EL SALVADOR. **Santa Ana**. Coatepeque, 3 Sep. 1994, *R. Villacorta 2198* (K); Santa Ana, P.N. Los Volcanes, sector Los Andes, sendero al crater, 1783 m, 13°52'N, 89°38'W, 26 May 2005, *J. Monterosa 918* (MO).

GUATEMALA. **Alta Verapaz**. 1906, *M. Gandoger s.n.* (G); **Petén**. Tikal National Park, growing in zapotal along Remate Road, 3 Jul. 1959, *C.L. Lundell 16146* (US); Tikal National Park, in secondary growth bordering airfield, 4 Aug. 1959, *E. Contreras 72* (G); Tikal National Park, 6 Aug. 1960, *E. Contreras 1395* (NY); Petén, Dos Lagunas, in zapotal, on Ixcandrio Road, 12 Oct. 1960, *E. Contreras 1518* (US); Dos Lagunas, bordering north lake, in low forest, 15 Dec. 1960, *E. Contreras 1689* (NY); Tikal National Park, Tikal on the top of temple II, 21 Jan. 1961, *E. Contreras 1846* (US); Uaxactum, 20 Dec. 1963, *E. Contreras 3641* (US); Ruinas Plaza Mayor en Tikal, 16 Nov. 1965, *A. Molina 15818* (US); Tikal, Sacate en camino para Uaxactum, 29 Jul. 1969, *R.T. Ortíz 204* (US); **Quezaltenango**. Colomba, 29 Sep. 1934, *A.F. Skutch 1345* (US).

HAITI. **L'Artibonite**. Vicinity of Ennery, Département de l'Artibonite, 325-900 m, 3 Feb. 1926, *E.C. Leonard 9466* (MO, US); **Gonave Island**. Vicinity of Anse Galette, Gonave Island, 11 Mar. 1920, *E.C. Leonard 3240* (NY, US), *3240* (BM); Vicinity of Pikmi, 5-9 Jul. 1920, *E.C. Leonard 5121* (NY); **Nord**. Port de Paix western slope of Haut Pibon in falaise at Rivière Froide, 26 Jun. 1925, *E.L. Ekman 4438* (US); Vicinity of St. Raphael, 350 m, 2 Dec. 1925, *E.C. Leonard 7650* (US); Vicinity of St. Louis du Nord, 30 Mar.-7 Apr. 1929, *E.C. Leonard & G.M. Leonard 14292* (NY); **Ouest**. Vicinity of Pétionville, 350 m, 25 Jun. 1920, *E.C. Leonard 5054* (BM, US); Port au Prince, hills between the town and Pétionville at Source Plaisance, 19 Oct. 1924, *E.L. Ekman 2190* (C, US); **Sud**. Arrondissement de Jéremie, southern peninsula, flood plain of Grand Rivère de Jérémie, 7 Jul. 1941, *H.H. Bartlett 17498* (US); Between Anse d'Hainault and Dame Marie, southern peninsula, 8 Jul. 1941, *H.H. Bartlett 17519* (US).

HONDURAS. **Comayagua**. Chichipates, orilla del Río Yure, 30 km E Lago Yojoa, 200 m, 22 Nov.-31 Dec. 1980, *C. Nelson & al. 6654* (MO); **Copán**. Vicinity of Santa Rita, 21 Aug. 1971, *A. Molina 26229* (BM, NY, US); Vicinity of Jaguar Temple of Copán, 3 Jan. 1990, *A. Molina & Albertina R. 34261* (US); **Cortés**. Montaña de Río Piedras, 4 Dec. 1950, *A. Molina 3541* (BM, MO, US); 5 km of San Pedro Pula, Río Arenales, El Sauce, 18 Dec. 1950, *A. Molina 3814* (BM, US); **Santa Barbara**. El Nispero, 25 km al S de la ciudad de Santa Barbara cercanías del proyecto hidroeléctrico, 600-800 m, 8 Aug. 1982, *G. Padilla 48* (MO); Lago Yojoa, Punta Gorda, 650 m, 14°52'N, 88°00'W, 2 Nov. 1988, *J.M. McDougal & al. 3125* (MO); **Yoro**. 19 km SE of Río Viejo, 27 Jun. 1970, *G. Davidse & R.W. Pohl 2200* (K, MO, NY, US), **n = 18!** (Davidse 1978).

JAMAICA. *C. Wright s.n.* (K); **Clarendon**. Upper slopes of Round Hill, 900-1000 ft, 26 Jul. 1979, *G.R. Proctor 38265* (FTG, MO); **Middlesex**. 28 Jan. 1938, *F.W. Hunnewell 15226* (NY); **Portland**. St. Margaret Bay, 6 miles W of Port Antonio, 18 Feb. 1906, *A.E. Wight 118* (NY); **St. Andrew**. Stony Hill Road, above Constant Spring, near Kingston, 25 Sep. 1912, *A.S. Hitchcock 590* (BM, C, G, K, L, MO, NY, P, US, W); Hells' Delight, roadside, 10 Oct. 1912, *W. Harris 11260* (BM, C, K, NY, P, US); Road from Pardon Source to Flamstead, 26 Nov. 1912, *W. Harris 11454* (BM, K, MO, NY, P, US); Blue Mts., Mount Faraway, 3 Dec. 1912, *W. Harris 11490* (P); Bryans Hill, 26 Dec. 1912, *W. Harris 11531* (NY, US); St Andrew, hill just above Yallahs River Bridge below Chestervale, 850 m, 24 Nov. 1971, *G. Davidse & G. Proctor 3249* (MO, US); **St. Ann**. 1.4 miles S of Ocho Ríos at end of Fern Gully, 130 m, 26 Nov. 1971, *G. Davidse & E. Convoy 3273* (MO, NY, US); **St. Catherine**. Between Bog Walk and Spanish Town, 26 Sep. 1912, *A.S. Hitchcock 591* (BM, C, G, K, L, MO, NY, P, US, W); Ewarton to Linstead, 9-11 Oct. 1912, *A.S. Hitchcock 9413* (US); Blue Mts., Pimento Grove, 22 Jan. 1913, *W. Harris 11589* (BM, NY); Bog Walk and vicinity, 27 Jul. 1926, *W.R. Maxon 10502* (NY, US); **St. Elizabeth**. Santa Cruz Mountains, 9 Sep. 1907, *N.L. Britton 1280* (NY); Ipswich to Black River, 21 Oct. 1912, *A.S. Hitchcock 9606* (US); **St. James**. Montego Bay, Mar. 1916, *H.N. Ridley 35* (US); Orange River, near Montego Bay, 29-30 Mar. 1920, *W.R. Maxon & E.P. Killip 1673* (NY, US); **St. Thomas**. 2.4 miles SE of Cedar Valley along road to Seaforth, 350 m, 25 Nov. 1971, *G. Davidse & E. Convoy 3264* (MO); **Trelawny**. Troy, 6 Nov. 1912, *A.S. Hitchcock 9801* (US).

LEEWARD ISLANDS. **Antigua**. Forest NE of Dark Valley, below Boggy Peak, 16 Dec. 1931, *H.E. Box 119* (BM, K, US); **St. Martín**. Pic du Paradis, sommet, 424 m, 7 Dec. 1977, *A.M. Raynal 19643* (P).

MEXICO. **Campeche**. Zuxpeña, Campeche, 6 Nov. 1931, *C.L. Lundell 904* (K, MO, NY, US); Calakmul, loc. a 4 km al S de La Nueva Vida, camino a Xpujil, en el puente Papagayo, 297 m, 18°44'15"N, 89°23'32"W, 2 Aug. 1997, *E. Martínez S. 27983* (MO); Campeche, Municipio Calakmul, a 34 Km al S de la Caseta de entrada a Calakmul, 160 m, 18°15'47"N, 89°49'39"W, 18 Oct. 1997, *E. Madrid 292* (BM, MO); Campeche, Calakmul, road to Nadzcaan, 195 m, 18°33'21"N, 89°53'49"W, 23 Oct. 2002, *D. Àlvarez 2184* (BM, MO); **Chiapas**. Hillside 3 km W of the Chiapas/Tabasco border on Highway 186, 19 Aug. 1974, *J. Conrad & R. Conrad 2986* (K, NY); Ocosingo, Lower Montane Rain Forest, 70 km SW of Palenque on road to Ocosingo along the Jol uk'um, 9 Nov. 1981, *D.E. Breedlove 55237* (NY); Along Highway 195 between Chiapa de Corzo and Pichucalco, 10.7 miles S of Solosuchiapa, 27.8 miles SSE of Pichucalco, 520 m, 17°23'N, 93°00'W, 18 Feb. 1987, *T.B. Croat & D.P. Hannon 65305* (MO); Aeropuerto-Ocozocoautla-México, 17 Sep. 1988, *A. Reyes García 969* (BM, MO); Angel Albino Corzo, 13 Nov. 1989, *A. Reyes García & al. 1414* (BM); Ocosingo, 2 km al E de Nuevo Guerrero, 22 m, 16°58'35"N, 91°16'09"W, 5 May 2002, *J.C. Soto 23284* (MO); Ocosingo, banco de grava de San Javier, 560 m, 16°48'10"N, 91°05'43"W, 13 Aug. 2002, *E. Martinez & al. 35679* (BM, MO); **Colíma**. Manzanillo, 19 Sep. 1910, *A.S. Hitchcock 410* (BM, G, L, MO, NY, P, US, W); **Hidalgo**. On Highway below Chapulhuacan, 26 Sep. 1946, *H.E. Moore 1328* (US); **Oaxaca**. 5 km S of Tuxtepec, 30 Aug. 1974, *J. Conrad & R. Conrad 3253* (K, MO, US); 8 miles NE of Valle Nacional on Highway 175 to Tuxtepec, 16 Aug. 1975, *G.& J. Davidse 9732* (K, MO, US), **n = 18!** (Davidse 1978); En los alrededores de las Bombas de Auxiliación de la Presa de Temaxcal, 22 Sep. 1984, *E. Cabrera 7232* (MO); **Quintana Roo**. Tancah, 4-5 Aug. 1932, *J.R. Swallen 2807, 2817* (US); Quintana Roo, F. Carrillo Puerto, 16 Nov. 1980, *E. Cabrera 393* (BM); **San Louis Potosí**. Ledges, Tamasopo Canyon, 1 Jul. 1890, *C.G. Pringle 3403* (US); Las Canoas, 15 Aug. 1891, *C.G. Pringle 3808* (NY, US); Tamasopo, 8-9 Aug. 1934, *F.W. Pennell 18012* (US); Tamazunchale, 5 Aug. 1937, *G.L. Fisher 37127* (MO, NY), *37129* (US); In a tropical forest between Narango-Platinito-Salto de Agua, 22 Sep. 1954, *E.R. Sohns 1406* (K, US); 9 miles E of Xilitla, 18 Jul. 1963, *R.L. McGregor & al. 933* (US); 1.5 km SW of Tamazunchale on Highway 85, 150 m, 26 Oct. 1985, *B. Bartholomew 3* (MO); **Tabasco**. Arriba de las grutas del Cocona, a 2 km de Teapa, 8 Sep. 1980, *C. Cowan 3153* (MO, NY); Teapa, E of Chapingo, 28 Jan. 2002, *Calónico & al. 21134* (BM); **Tamaulipas**. 10 km NW of El Progreso, 30 Aug. 1941, *L.R. Stanford & al. 1061* (MO, NY); Western slopes of the Sierra de Tamaulipas at Santa Maria de los Nogales, 800 m, 23 Sep. 1956, *F.M. Martinez & G.B. Luyando F-2102* (US); **Veracruz**. Coatepec, 3 km de Tuzamapa, 19°22'N, 96°53'W, *M. Vasquez Torres 2238* (MO); **Yucatán**. Yucatán, Chichen Itzá, 7-13 Jul. 1932, *J.R. Swallen 2415* (K, US); Tizimin, 14-16 Jul. 1932, *J.R. Swallen 2519* (K, US); Yucatán, Peto, 26-27 Jul. 1932, *J.R. Swallen 2714* (K, US).

NICARAGUA. **Carazo**. Jinotepe, 3-7 Nov. 1911, *A.S. Hitchcock 8673* (NY, US), *8700* (US); **Chontales**. 12 km E of Villa Somoza along Highway 7, 18 Jul. 1970, *G. Davidse & R.W. Pohl 2388* (MO, US); 3 km N of Cuapa, 500 m, 3 Sep. 1977, *D. Neill 2515* (MO); **Granada**. NE del Volcán Mombacho, Hacienda Las Delicias, de 8-9 km sobre la carretera a Cutirre, 350-400 m, 11°51'N, 85°58'W, 16 Sep. 1980, *P. Moreno 2673* (MO).

PANAMA. **Panamá**. s.d., *s.coll.* (Exp. Malaspina), sec. XVIII, *L. Nèe s.n.* (MA); Parque Nacional Altos de Campana, despues del mirador del Parque, 642 m, 8°41'22"N, 79°54'54"W, 14 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 815* (FT, PMA, SCZ); Parque Nacional Altos de Campana, Capira, 29 Jan. 2013, *O.O. Ortiz & R.M. Baldini 1988* (FT, PMA); Parque Nacional Altos de Campana, carretera a Chicá, 8°41'13"N, 79°55'W, 2 Feb. 2014, *M.N.S. Stapf & R.M. Baldini 939* (FT, PMA).

PUERTO RICO. 1827, *H. Wydler 222* (FI-Webb); Toa Alta, 11 Nov. 1960, *R. Woodbury s.n.* (NY).

SURINAME. Bei Paramaribo, 1913, *J. Kuiper 27915* (L).

VENEZUELA. **Aragua**. 16.3 km NW of Rancho Grande along road to Cata, 270 m, 15 Nov. 1971, *G. Davidse 3116* (MO); **Bolívar**. Upper part of west-facing wooded slopes, E of Miamo, Altiplanicie Nuria, 300-500 m, 8 Jan. 1961, *J.A. Steyermark 88189* (NY, US); **Bolívar**. El Pao Viejo, 430 m, 7 Dec. 1973, *G. Davidse & al. 4969* (K, MO, US); **Lara**. Alredadores de Barquisimeto, Jul. 1925, *J. Saer d'Héguert 280* (G, NY, US); **Mérida**. Tovar, penetration road to Mijagual from 1 km S of Puente Victoria, 600-800 m, 29 Aug. 1973, *S.S. Tillet & K.W. Hönig 738-549* (MO); **Miranda**. Plaza, campamento Scout Curupao, al NE de Guarenas, 10°30'N, 66°39'W, 400-600 m, 19 Sep. 2008, *W. Meier & C. Bottome 15180* (G); **Táchira**. Vicinity of San Cristóbal, 5 Jan.-22 Feb. 1923, *W.E. Broadway 289* (US).

(19) *Lasiacis standleyi* Hitchc., Proc. Biol. Soc. Wash. 40: 86. 1927. (Fig. 48, 49).

Type: "*Costa Rica, Guanacaste, La Tejona, north of Tilaran, moist forest, subscandent, 8 ft, 600-700 m, 25 Jan. 1926, P.C. Standley & J. Valerio 45839*" (holotype: US! [barcode US00134122]; isotype MO! [Acc. No. MO354963]).

(=) *Lasiacis lucida* Swallen, Ann. Missouri Bot. Gard. 30: 231. 1943.

Type: "*Panamá, Chiriquí, Volcán de Chiriquí, forest above Sabana de El Salto, on trail to Camp Aguacatal, eastern slope of Chiriquí Volcano, altitude 1500 to 1750 m, 10-13 March 1911, W.R. Maxon 5266*" (holotype: US! [barcode US00134114]; isotypes L! [barcode L0797287]! US! Two sheets [barcode US00134112, US00134113]).

(=) *Lasiacis longiligula* Swallen, Ann. Missouri Bot. Gard. 30: 232. 1943.

Type: "*Panamá, Canal Zone, forest along telephone cable trail between splice S16 and S49, Río Indio, trail toward Chico, 1m tall, 12 January 1935, J.A. Steyermark & P.H. Allen 17435*" (holotype: US! [barcode US00134111]; isotypes G! [barcode G00176063], GH (photo!) [barcode GH00023860], K! [barcode K001491992], MO! [Acc. No. MO354963]).

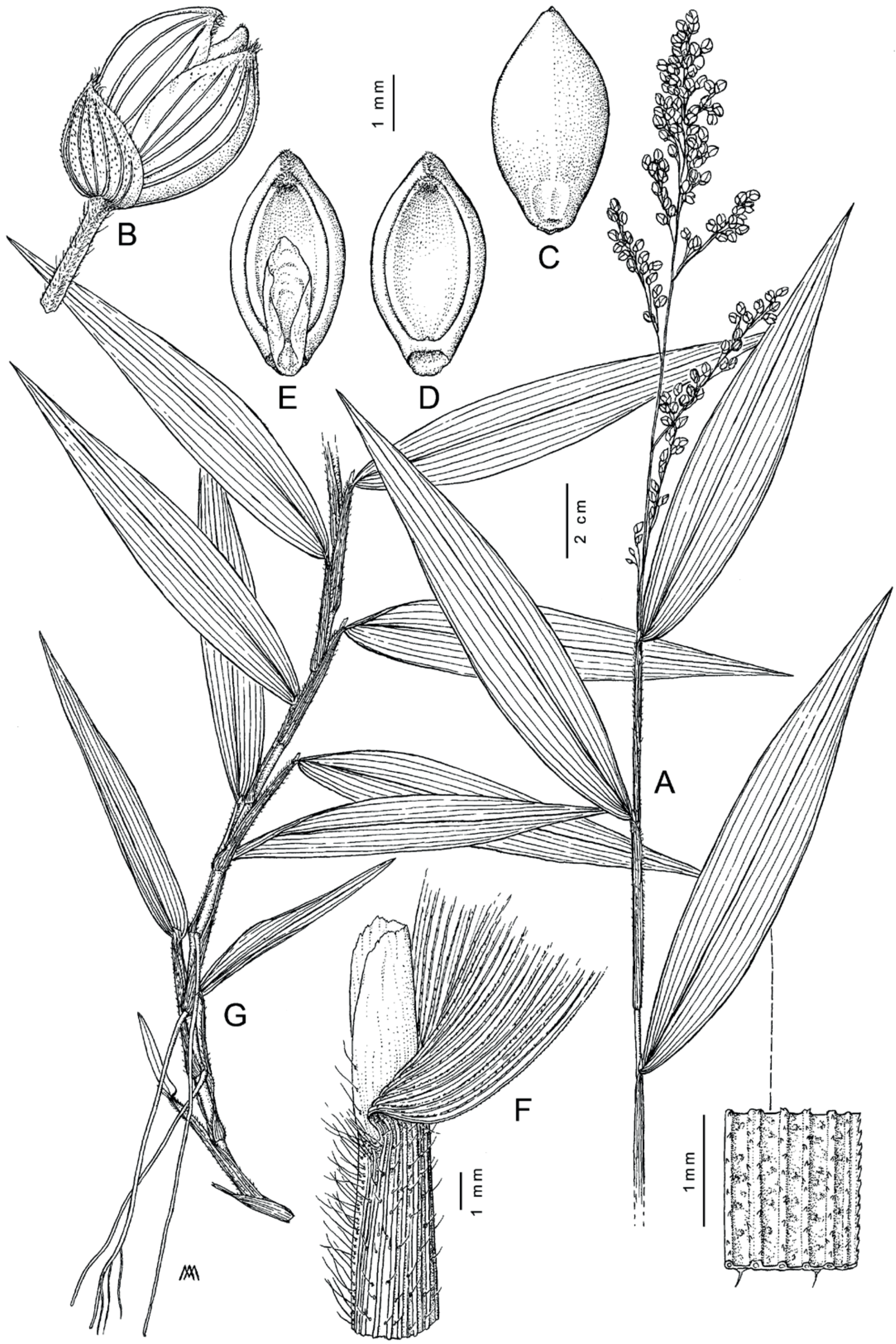

Figure 48. *Lasiacis standleyi* Hitchc.: **A**. Habit; **B**. Spikelet lateral view; **C**. Fertile upper floret dorsal view; **D**. Fertile upper floret ventral view without lower persistent palea; **E**. Fertile upper floret ventral view with lower persistent palea; **F**. Ligular area [A-F. from *P.H. Allen 1338* (K)]; **G.** Culm at the medium length rooting at the nodes [G. from *B.A. Stein & C.W. Hamilton 1149* (K)]. *A. Maury delineavit*.

Figure 49. *Lasiacis standleyi* Hitchc.: procumbent habit in shade forest (Panama, Chiriquí, photo R.M. Baldini).

Description

Perennials, semi-caespitose. Culms up to max 1 m tall, creeping, rooting at the nodes or erect usually scrambling into the shrubs up to several meters; *internodes* 2-5 mm thick, herbaceous, hollow, puberulent upward, often pubescent; *nodes* glabrous to puberulent. *Leaf sheaths* puberulent to pubescent, often hispid with hairs up to 3.0 mm long; *collars* glabrous; *ligules* 4.5-7.0(-8.0) mm long, conspicuous and prominent, membranous, lacerate, slightly ciliate at the base, usually glabrous on the back; *blades* 10-20 cm long, 1.5-3.5 cm wide, elliptic-lanceolate to linear, adaxial surface scabrous, rarely glabrous, adaxial surface puberulent to hispidulous, apex acuminate, base asymmetrical, margins scabrid, often undulate. *Panicles* up to 30 cm long, rather compact; *branches* ascending, often spreading; *pedicels* usually slightly pubescent, rarely scabrid. *Spikelets* 3.5-5.0 mm long, ovate-elliptic; *lower glumes* 1.8-2.5 mm long, 0.8-1.5 mm wide, 9-11-veined; *upper glumes* 1.8-3.8 mm long, 1.0-1.8 mm wide, 9-13-veined; *sterile florets* without flowers, *lemmas* 11-13-veined, *paleas* ½ the length of the fertile floret; *fertile florets* 3.5-4.3(-4.5) mm long, 2.0-2.5 mm wide, *anthers* 2.2 mm long, white or yellowish, *stigmas* purple; *caryopses* 2.0-2.5 mm long, 1.5-2.0 mm wide. *Chromosome number*: n = 18 (Davidse 1972, 1978).

Distribution

Belize, Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Perú, Venezuela. (Fig. 50).

Distribution (bibliographic references)

Hitchcock (1927, 1930); Standley (1937); Swallen (1931, 1943); Pohl (1980); D'Arcy (1987); Davidse (1978, 1994, 2001); Cialdella and Vega (1996); Serna and López-Ferrari (2000); Morales (2003); Zuloaga et al. (2003); Correa et al. 2004; Renvoize et al. (2006); Hokche et al. (2008); Sutherland (2008); Bono (2010); Giraldo-Cañas (2011); Villaseñor (2016); Dávila et al. (2018); Sánchez-Ken (2019).

Ecology

Common grass at edges of moist and wet undisturbed forests, in moist cloud forest openings and along trails in montane vegetation. Elevation between 500 m to 2200 m [Colombia: El Valle, *E.P. Killip & H. Garcia 33774* (US)].

Phenology

October through May, with the peak December through March.

Remarks

Lasiacis standleyi is a creeping species that grows in the forest undergrowth often in association with other species belonging to "Forest Shade Clade" such as *Acroceras zizanioides* (Kunth) Stapf, *Oplismenus burmannii* (Retz.) P.Beauv., *Oplismenus hirtellus* (L.) P.Beauv., *Pseudechinolaena polystachya* (Kunth) Stapf.

The hollow culm, short leaf blades, and long ligules are all distinctive characters. The presence of long ligules (up to 8 mm) can cause confusion with other species such as *L. oaxacensis*, *L. ligulata*, and *L. scabrior*.

The specimens collected by me in the area from where *L. lucida* Swallen was described (Panamá, Chiriquí, Volcán de Chiriquí) seem to be quite different and perhaps they might be worth of more attention at the population level.

Selected specimens

BELIZE. **Toledo**. Crique Negro, 14 Feb. 1951, *P.H. Gentle 7205* (BM); Toledo, Southern Maya Mountains, Bladen Nature Reserve, Ridge just S of the Main Divide of the Maya Mountains, "Augusta Divide Camp", 920 m, 16°29'22"N, 88°59'33"W, 22 May 1997, *G. Davidse & D.L. Holland 36712* (MO).

COLOMBIA. **Antioquia**. Amalfí, Vereda La Viborita, 4 km NO de Amalfí, 1500-1510 m, 6°55'N, 75°05'W, 8 Dec. 1989, *R. Callejas & al. 9190* (MO, NY); Las Orquideas, Vereda Calles, Quebrada Honda, 1330 m, 06°29'N, 76°14'W, 8 Dec. 1992, *J. Pipoly & al. 16833* (MO, NY); **Caldas**. Río Santa Rita, Salento, Cordillera Central, 1600-1800 m, 26 Aug. 1922, *E.P. Killip & T.E. Hazen 10138* (US); **Cauca**. Hills of Miraflores above Palmira, central Cordillera, 1200-1600 m, Jan. 1906, *H. Pittier 875* (US); Cauca, Río Hondo to Popayan, 1500-1700 m, 4 Jul. 1922, *E.P. Killip*

Figure 50. *Lasiacis standleyi* Hitchc.: general geographic distribution.

8259 (NY, US); Cauca. La Gallera Micay Valley, 1400-1500 m, 29-30 Jun. 1922, *E.P. Killip 7714* (NY, US); **Magdalena**. Santa Marta, 1898-1901, *H.H. Smith 2148* (G), *H.H. Smith 2258* (G, L, NY, P); **Meta**. Restrepo, Salinas, subida al cerro, 600-700 m, 12 Jun. 1989, *F.O. Zuloaga 3941* (US); **Putumayo**. Sachamates below mouth of Quebrada Patoyaco, Río Susunga (upper Río Mocca), 17 km W of Mocoa, 1600 m, 1°10'N, 76°47'W, 27-28 Mar. 1943, *F.R. Fosberg 20370* (US); **Valle**. Miraflores, Palmira, Cordillera Central, 1800-2100 m, 27 May 1922, *E.P. Killip 6149* (NY, US); El Silenzio, Yanaconas, 1900-2200 m, 28 Feb. 1939, *E.P. Killip & H. Garcia 33774* (US); Cordillera Occidental, Hoya del Río Sanjuniquín, lado izquierdo, La Laguna, 1250-1400 m, 10-20 Dec. 1943, *J. Cuatrecasas 15602* (US); Yotoco, Cordillera Occidental, eastern slopes, along Highway between Dapa and Loboguerrero at Parque Yotoco, 1485-1550 m, 03°52'N, 76°22'W, 17 Feb. 1990, *T.B. Croat 70702* (MO); Lago Calima, 6 Sep. 1992, *S.A. Renvoize 5364* (K) .

COSTA RICA. **Alajuela**. Vicinity of San Ramon, 21 Jan. 1935, *A.M. Brendes 20319* (NY); **Cartago**. Vicinity of Pejivalle, Jan. 1940, *A.F. Skutch 4571, 4649* (MO, NY, US); Along road between Navarro and El Muneco, along S side of Río Navarro, 9°48'N, 43°54'W, 1150 m, 15 Nov. 1987, *M. Grayum & B. Hammel 8430* (US); **Guanacaste**. Los Ayotes, near Tilarán, 600-700 m, 21 Jan. 1926, *P.C. Standley & J. Valerio 45532* (US); La Tejona, N of Tilarán, 600-700 m, 25 Jan. 1926, *P.C. Standley & J. Valerio 45820* (US); Lower forested slopes of Volcán Orosí at the hacienda Los Inocentes about 15 km SE of La Cruz at an elevation of between 650-2100 feet, 26 Mar. 1968, *R.L. Wilbur & D.E. Stone 10214* (MO, PMA); Cordillera de Talamanca, Volcán Rincón de La Vieja, Hacienda Guachipelin, 900 m, 17 Jan. 1969, *R.W. Pohl & G. Davidse 11675* (MO); Parque Nacional Rincón de la Vieja, the SE slopes of Volcán Santa María, 27-28 Jan. 1983, *G. Davidse & al. 23354* (K, MO); Guanacaste, ridge SE of Quebrada Zopilote, lower SE slope of Volcán Santa María, 950-1000 m, 10°46'N, 85°18'W, 24 Jan. 1986, *M.H. Grayum & al. 6208* (MO); **Heredia**. Yerba Buena, NE of San Isidro, 2000 m, 22-28 Feb. 1926, *P.C. Standley & J. Valerio 49785, 50068* (US); Vera Blanca de Sarapiquí, north slope of Central Cordillera, between Pos and Barba Volcanoes, Mar. 1938, *A.F. Skutch 3674, 3680* (K, MO, NY); **Limón**. Talamanca, Coroma, 31 May 1977, *Rafael & Ocampo 1686* (K); **Puntarenas**. Slopes up high road from Rincon, Península de Osa, 650 m, 3 Mar. 1965, *R.K. Godfrey 66916* (NY, US); Forested slopes E of Las Cruces and 5 to 6 km S of San Vito on and around the property of Mr Robt. Wilson, 8°47'N, 82°58'W, 15-16 Jan. 1967, *W.C. Burger & G. Matta 4482*

(NY, US); Primary forest and forest edge, Finca Loma Linda, 1 mile SW of Cañas Gordas, 1150 m, 26-27 Feb. 1973, *T.B. Croat 4482* (US); Cantón de Puntarenas, Monteverde, 1350 m, 10°18'N, 84°48'W, 14 Dec. 1989, *W.A. Haber 9609* (MO); Cantón de Osa, Agua Buena, Rincón, 60-70 m, 8°41'32"N, 83°30'21"W, 23 Jan. 1991, *V. Ramírez 248* (USJ); Parque Nacional Corcovado, Cerro Brujo, 600 m, 8°38'N, 83°35'W, 24 Jan. 1991, *E. Castro 252* (MO, USJ); 29 km NE of San Vito de Java near Alturas, 10 Jan. 1992, *J.R. Grant & J.R. Rundell 1824* (US); San Vito de Coto Bus, Jardín Botánico Wilson Sendero Java, 8°47'9"N, 82°57'29.3"W, 28 Jan. 1999, *T. Bermúdez 66* (USJ); Buenos Aires, P.N. La Amistad, Cuenca Terraba-Sierpe, Buenos Aires, Portero Grande, Tres Colinas, 1700-1800 m, 9°08'10"N, 83°03'22"W, 29 Feb. 2008, *D. Solano 5253* (MO); **San José**. Vicinity of El General, Dec. 1935, *A.F. Skutch 2206* (K, MO, NY, US); Vicinity of El General, Jan. 1939, *A.F. Skutch 3802* (K, MO, NY, US); Eastern spur ridge of Cerro Hondura, between Río Patria and Río Zurquí, Cordillera Central, 10°04'N, 84°01'W, 1500-1600 m, disturbed sites, 18 Jan. 1986, *M.H. Grayum & P. Sleeper 6118* (MO, US); Cantón de Perez Zeledon, ca. 15 km S de San Isidro, El Pilar de Cajon, 600 m, 9°17'00"N, 83°37'00"W, 4 Feb. 1991, *B. Hammel & al. 18054* (MO); Pérez Zeledón, Río Nuevo, Finca de Julio Mena, 9°27'20"N, 83°50'30"W, 10 Feb. 1999, *A. Estrada & al. 2029* (K, USJ); Pérez Zeledón, Río Nuevo, Savegre Abajo, 6 Feb. 2001, *A. Estrada 2684* (K).

ECUADOR. **Napo-Pastaza**. Vicinity of Puyo, 750-1000 m, Aug. 1939, *A.F. Skutch 4460* (K, MO, NY, US); **Tungurahua**. Valley of Pastaza River, between Banhos and Cashurco, 8 hours of Banhos, 1300-1800 m, 25 Sep. 1923, *A.S. Hitchcock 21894* (NY, US); Valley of Río Pastaza, between Machai and La Victoria, 1400 m, 24 Aug. 1939, *E. Asplund 8514* (MO, NY, US).

EL SALVADOR. **Santa Ana**. Parque Nacional Montecristo, 3 Sep. 2002, *R.A. Carballo 444* (BM).

GUATEMALA. **Huehuetenango**. Barillas, Aldea Malpais, secondary cloud forest on volcanic soil, 1200 m, 15°51'N, 91°13'W, 1 Mar. 2009, *J.M. Maarten & al. 5426* (MO); **Petén**. Sacate, Dolores, en el camino para-Río Machaquilla, en km 85, 15 Feb. 1971, *R.T. Ortíz 1576* (F, SCZ, US).

HONDURAS. Atlantida. Sobre árboles en el bosque lluvioso de Montana Lancetilla, cerca de El Portello, 3 km al sur de Lancetilla, 19 Mar. 1962, *A. Molina 10467* (US); **Cortés**. Mountains on N side of Lake Yojoa, in rainforest, 10 Apr. 1951, *C.V. Morton 7619* (NY, US); **Lempira**. Near Gracias, Montaña de Celaque, 20 Sep. 1991, *M. Chorley 342 pro parte* (BM); **Olancho**. Road from San Francisco de La Paz to Gualaco, 11.5 km S of Gualaco, 1000 m, 14°57'N, 86°08'W, 29 May 1992, *W.G. D'Arcy 18050* (MO).

MEXICO. **Chiapas**. Ocozocoautla de Espinosa, steep heavily wooded slope, 32 Km N of Ocozocoautla along road to Mal Paso, 2500 ft, 19 Oct. 1965, *D.E. Breedlove & P.H. Raven 13566* (US); Ocosingo, 5 km SW of Santo Domingo, 13 May 1982, *G. Davidse & al. 20448* (BM); Ocosingo, en Laguna Ocotalito a 12 km al N de Monte Libano camino a Chancala, 980 m, 2 Feb. 1986, *E.M. Martínez S. 17189* (MO); Ocosingo, a 2.5 km al N de San Javier, 16°27'43"N, 91°14'26"W, 21 Dec. 2002, *G. Aguilar 4822* (NY); **Tabasco**. Huimanguillo, Cabañas Agua-Selva W of Malpasito, 31 Jan. 2002, *E.M. Martínez S. & al. 34787* (BM); **Veracruz**. Hidalgotitlán, north side of Río Solosúchil, 2-3 km SE of Augustin Melgar, 17°14'N, 94°33'W, 5 Mar. 1984, *M. Nee & K. Taylor 29937* (NY).

NICARAGUA. **Granada**. Upper slope of Volcán Mambacho along W shore of Lake Nicaragua, ca. 15 km S of Granada, 1100-1200 m, 19 Mar. 1977, *T.B. Croat 39093* (MO); **Jinotega**. Macizos de Peñas Blancas, along trail between finca of Socorro Mejia and finca of Luis Manzanares, 1350-1650 m, 13°17'N, 85°41'W, 14 Jan. 1979, *W.D. Stevens & al. 11373* (MO); Wiwili, Reseva Natural Kilambé, Comunidad Aguas Frias, Sector Caballo Blanco, 900-1200 m, 13°35'N, 85°44'W, 25 May 2001, *R. Rueda & al. 16351* (MO); Wiwili, Comunidad La Esperanza, Reserva Bosawas, Territorio Miskito, Indian Tasbaika Kum, parcela 2 en el Tacotal, 500 m al oeste de la Finca de Lionidas, 60-70 m, 25 Feb. 2008, *C. Centeno 248* (MO); **Matagalpa**. Road to La Fundadora, N of Maria de Ostuma, Feb. 1963, *L.O. Williams & al. 24919* (G, NY, W); **Rivas**. Isla de Omotepe, San Pedro, al E del Volcán Maderas, 200-450 m, 11°25'N, 85°28'W, 2 Mar. 1983, *J.C. Sandino 4283* (MO); **Zelaya**. Along rail from Cerro El Inocente toward Cerro Saslaya, 1050-1150 m, 13°46'N, 85°00'W, 8 Mar. 1978, *W.D. Stevens & al. 6708* (MO); Siuna, Reserva Bosawas, Cerro Saslaya, 800-1000 m, 13°47'N, 84°59'W, 14 Apr. 1999, *R. Rueda & al. 10699* (MO).

PANAMA. Bocas del Toro. 1525 m, 9°03'96"N, 82°43'93"W, 10 Mar. 2004, *E. Alfaro & A.K. Monro* 5475 (BM, PMA); Changuinola, PILA, Point 17, ca 2 km from éstacion de Alto Urí, 9°03'54"N, 82°42'006"W, 19 Apr. 2008, *D. Santamaria 7441* (PMA); Changuinola, PILA, 9°03'22"N, 82°42'15"W, 1450 m, 21 Apr. 2008, *J. Lezcano 330* (PMA); Changuinola, Cerro Frio, Cabeceras del Río Tskui, Punto 14, 1276 m, 9°25'45"N, 82°50'53"W, 25 Oct. 2008, *F. González 753* (MO); Changuinola, Bonyic, sitio presa, 9°17'12"N, 8239'01", 258 m, 3 Feb. 2014, *O.O. Ortiz & R.M. Baldini 2026* (FT, PMA); **Chiriquí**. Foothills vicinity of El Boquete, 1000-1300 m, 28 Sep.–7 Oct. 1911, *A.S. Hitchcock 8267* (US); Cerro Vaca, in forest or in thickets, 900-1200 m, 25-28 Dec. 1911, *H. Pittier 5339* (US); Open woods along Río Caldera 2 miles above El Boquete, 14 Feb. 1918, *E.P. Killip 4529* (US); "New Switzerland", central valley of Río Chiriquí Viejo, 6-14 Jan. 1939, *P.H. Allen 1338* (K, MO, NY); 1 mile E of Cañas Gordas on road to Volcán, near Costa Rican border), 26 Feb. 1973, *T.B. Croat 22331* (MO); N of Bambito, 4.5 km by air WNW of town of Cerro Punta, 2100 m, 8°52'N, 82°37'W, 3 Jan. 1975, *T.S. Cochrane & al. 6296* (MO); Above San Felix along mining road 18-27 miles off of Panamerican Highway (above Chame or turnoff to Escopeta), 1200-1500 m, 12 Mar. 1976, *T.B. Croat 33047* (MO); Ridge road at Cerro Colorado, 1450-1750 m, 15 Aug. 1977, *J.P. Folsom 4845* (MO, PMA); Near Fortuna Dam Camp, 25 Feb. 1985, *R.J. Hampshire & C. Whitefoord 59* (BM); Between Los Planes de Hornito and Fortuna Lake, 17 Mar. 1985, *R.J. Hampshire & C. Whitefoord 700* (BM); Along trail to Cerro Pate Macho, 1500-1700 m, 8°49'N, 82°24'W, 6 Feb. 1986, *G. MacPherson & M. Merello 8290* (MO); Ojo de Agua, vicinity of Santa Clara, between Volcán and Río Sereno, E of Volcán, 1520 m, 8°51'N, 82°45'W, 16 Jun. 1987, *T.B. Croat 66260A* (MO); Comarca Ngobe Buglé, corregimiento de Hato Chami, base de Cerro Flores, 8°29'06"N, 81°46'13"W, 1441 m, 22 Jan. 2008, *M.N.S. Stapf & al. 554* (FT, PMA); Sendero del Pianista, 8°49'08"N, 82°25'20"W, 1404 m, 11 Jul. 2012, *O.O. Ortiz 783* (PMA); **Colón**. Along Santa Rita ridge road, 9°20'N, 79°45'W, 500 m, 16 Feb. 1986, *G. MacPherson 8442* (MO, PMA); **Darién**. West ridge of Cerro Mali due West of helipad on trail to Río Pucro valley, premontane wet forest, 1150-1350 m, 23 Jan. 1975, *A. Gentry & S. Mori 13855* (MO, NY, PMA); Cerro Tacaruna, W ridge 1500-1550 m, 2 Feb. 1975, *A. Gentry & S. Mori 14090* (MO, PMA); Darién, east slope of Cerro Sapo, 2500 ft, 3 Feb. 1978, *B. Hammel 1310* (MO); Alto de Nique, S peak of Cerro Pirre massif, 1300-1520 m, cloud forest on Panamá/Colombia border, 19 Apr. 1980, *A. Gentry & al. 28662* (MO, PMA); Serrania del Sapo, area surrounding Río Chado, 400 m, 7°40'N, 78°10'W, 2

Jan. 1981, *W. Hahn 253* (MO); 10 km NE of Jaque, headwaters of Río Pavarandó, 1400 ft, 31 Jan. 1981, *P. D'Arcy & K.J. Sytsma 14521* (BM, MO); Chepigana, Parque Nacional Darién, Río Casa Vieja, Darién, 7°59'24"N, 78°22'34"W, 676 m, 12 Apr. 2014, *O.O. Ortiz & al. 2303* (FT, PMA); Chepigana, Parque Nacional Darién, camino hacia la cima de Cerro Sapo, 7°58'40"N, 78°21'31"W, 891 m, 15 Apr. 2014, *O.O. Ortiz & al. 2348* (FT, PMA); **Herrera**. Hill above Chepo de Las Minas, 700 m, 19 Dec. 1977, *J.P. Folsom 6996* (MO, PMA); Between Las Minas and El Toro, near village of Chepo, trail along ridge of Motosa de Chepo Forest, 900-950 m, 7°42'04"N, 80°51'04"W, 24 Jan. 1987, *G. MacPherson 10289A* (MO, PMA); **Los Santos**. Vicinity of headwaters of Río Pedregal, 25 miles SW of Tonosí, 2500-3000 ft, 7 Dec. 1967, *W.H. Lewis & al. 2896* (MO); **Panamá**. Canal Zone, vicinity W end of Gatun Lake dam, 22 Dec. 1965, *K.E. Blum & E. Tyson 7268* (USJ); Slopes of Cerro Campana, about 2700 ft, 23 Jan. 1970, *R.L. Wilbur & R.E. Weaver 11300* (MO); Cerro Jefe, 2900 ft, 1 Jan. 1972, *A. Gentry 3515* (MO); Cerro Campana, 850 m, 11 Mar. 1973, *T.B. Croat 22784* (K, MO, US); La Eneida, ca. 10 km N of Goofy Lake, 675 m, 15 Jan. 1973, *T.R. Soderstrom 2007* (K, MO, US); 3 miles NE of Altos de Pacora, 500-800 m, 10 Mar. 1973, *R.L. Liesner 527* (MO); Premontane wet forest area, 6.5 km by road N of Lago Cerro Azul, 650-730 m, 13 Jan. 1974, *M. Nee 9295* (MO, PMA); Cerro Campana, 2700-2900 ft, 14 Feb. 1981, *K.J. Sytsma 3531* (BM, MO); In high ridges of the Serranda de Magé, S of the village of Ipetí, ca. 5 hrs walk from the village, tropical wet forest, 650-800 m, 31 Mar. 1982, *M. Huft & al. 1667* (MO, PMA); Parque Nacional Cerro Campana, 850 m, 8°42'N, 79°55'W, 1 Jan. 1983, *B.A. Stein & C.W. Hamilton 1149* (K, MO); Serranda de Majé, forest at top of ridge at headwaters of the Río Ipetí Grande, 100 m, 8°51'N, 78°34'W, 25-26 Jan. 1984, *H.W. Churchill & G. de Nevers 4342* (MO, PMA); Capira, Parque Nacional Altos de Campana, Sendero de Interpretación, 8°40'54"N, 79°55'40"W, 500 m, 27 Jan. 1990, *C. Galdames & al. 484* (PMA); Parque Nacional Altos de Campana, Buena Vista, Bejuco, 08°41'821"W, 079°57'791"N, 24 Feb. 1999, *F. Espinoza A. & L. Martinez 3451* (PMA); Parque Nacional La Campana, Cerro Campana in the Mirador on La Cruz trail, 780 m, 8 Apr. 2002, *J.G. Sanchez-Ken 679* (PMA); Cerro Azul, 4 km después del Lago Gofy, 9°11'15"N, 79°24'20"W, 706 m, 13 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 795* (FT, PMA, SCZ); Parco Nacional Altos de Campana, inicio del Sendero Panamá, 8°40'57"N 79°55'42"W, 889 m, 14 Jan. 2012, *M.N.S. Stapf & R.M. Baldini 804* (FT, PMA, SCZ); **Veraguas**. NW of Santa Fé, 1,5 km from Escuela Agricola Alto de Pietra, 29 Mar. 1975, *S. Mori & J. Kallunki 5315* (MO, US); Ridge of Cordillera de Tute, along tail to Cerro Tute, ca. 3-4 km past Escuela Agrícola Alto de Pietra, just W of Santa Fé, pre-montane and montane rainforest, 800-1400 m, 8°32'N, 81°07'W, 20 Mar. 1982, *S. Knapp & W.J. Kress 4383* (MO, PMA).

PERÚ. **Junín**. Gran Pajonal, Mapari, ca. 12 km SW of Chequitavo, 1300 m, 10°45'S, 74°23'W, 7 Apr. 1984, *H.H. Smith 6806* (K, MO); **San Martín**. Rioja, Pedro Ruíz-Moyobamba road, km 390, Venceremos, 1800 m, 77°45'W, 5°50'S, 27 Jul. 1983, *D.H. Smith 4407* (K, L, MO, US).

VENEZUELA. **Trujillo**. Along quebradas Los Riitos, Edo. Trujillo, slva virgen, arriba de Escuque, entre Escuque y la Mesa de San Pedro, 1300-1650 m, 20-23 Feb. 1971, *J.A. Steyermark 104658* (P, VEN); **Zulia**. Sierra de Perirá, a o largo de la quebrada del Río Omira-kuná, cerca de la frontiera Colombo-Venezolana, SE de Pishikakao e Iría, Mar. 1972, *J.A. Steyermark & al. 105551* (MO, P).

(20) *Lasiacis velutina* Swallen, Ceiba 4: 288. 1955. (Fig. 51).

Type: "*Honduras, Morazan, vicinity of El Zamorano, road to San Antonio, 17 October 1951, J.R. Swallen 10834*" (holotype: US! [barcode US00134123]; isotype MO! [Acc. No. MO2932156]).

(≡) *Lasiacis ruscifolia* (Kunth) Hitchc. var. *velutina* (Swallen) Davidse, Ann. Missouri Bot. Gard. 64: 375. 1977.

Description

Perennials, caespitose. *Culms* 2-5(-6) m tall, erect at the base or laying on vegetation, glabrous, sparingly branching, often rooting at nodes; *internodes* 2.8-6.8 mm thick, lignified, glabrous or with a line of hairs; *nodes* glabrous. *Leaf sheaths* pilose-velutinous, overlapping margin and throat ciliate; *collars* pilose; *ligules* 0.2-0.5 mm long, inconspicuous or roundly ciliolate; *blades* 5-7 cm long, 0.5-3.0 cm wide, ovate to ovate-lanceolate, adaxial surface hispid to velutinous, often pilose, abaxial surface softly pilose, base usually asymmetrical, ciliate, apex acuminate. *Panicles* 4-15 cm long, lower portion enfolded in the sheath or exserted; *longest branches* up to 7-8 cm long, terminal branch of each spikelet densely pilose to pubescent. *Spikelets* 3-4 mm long, globose, purple when immature; *lower glumes* 1.2-2.0 mm long, 7-10-veined; *upper glumes* 10-15(-16)-veined; *sterile florets* staminate, *lemmas* 8-12-veined, *paleas* subequal the length of the fertile floret, clearly acuminate at the apex and enrolled at the base; *fertile florets* 3.3-4.0 mm long, 2.3-2.5 mm wide, *anthers* 2.2-2.5 mm long; *stigmas* purple; *caryopses* 2 mm long, 1.8 mm wide. *Chromosome number*: $n = 18$ (Davidse 1972, 1978 as *L. ruscifolia* var. *velutina*).

Vernacular names

Honduras: El Paraiso, "*carrizo*" *A. Molina 4051* (US).

Distribution

Colombia, Costa Rica, Cuba, El Salvador, Honduras, Mexico, Nicaragua, Venezuela. (Fig. 52).

Distribution (bibliographic references)

Swallen (1955a); Davidse (1977, 1978, 1994, 2001); Morales (2003); Zuloaga et al. (2003); Sutherland (2008); Sánchez-Ken (2019). Note: Sánchez-Ken (2019) reports this species in Mexico (Chihuahua).

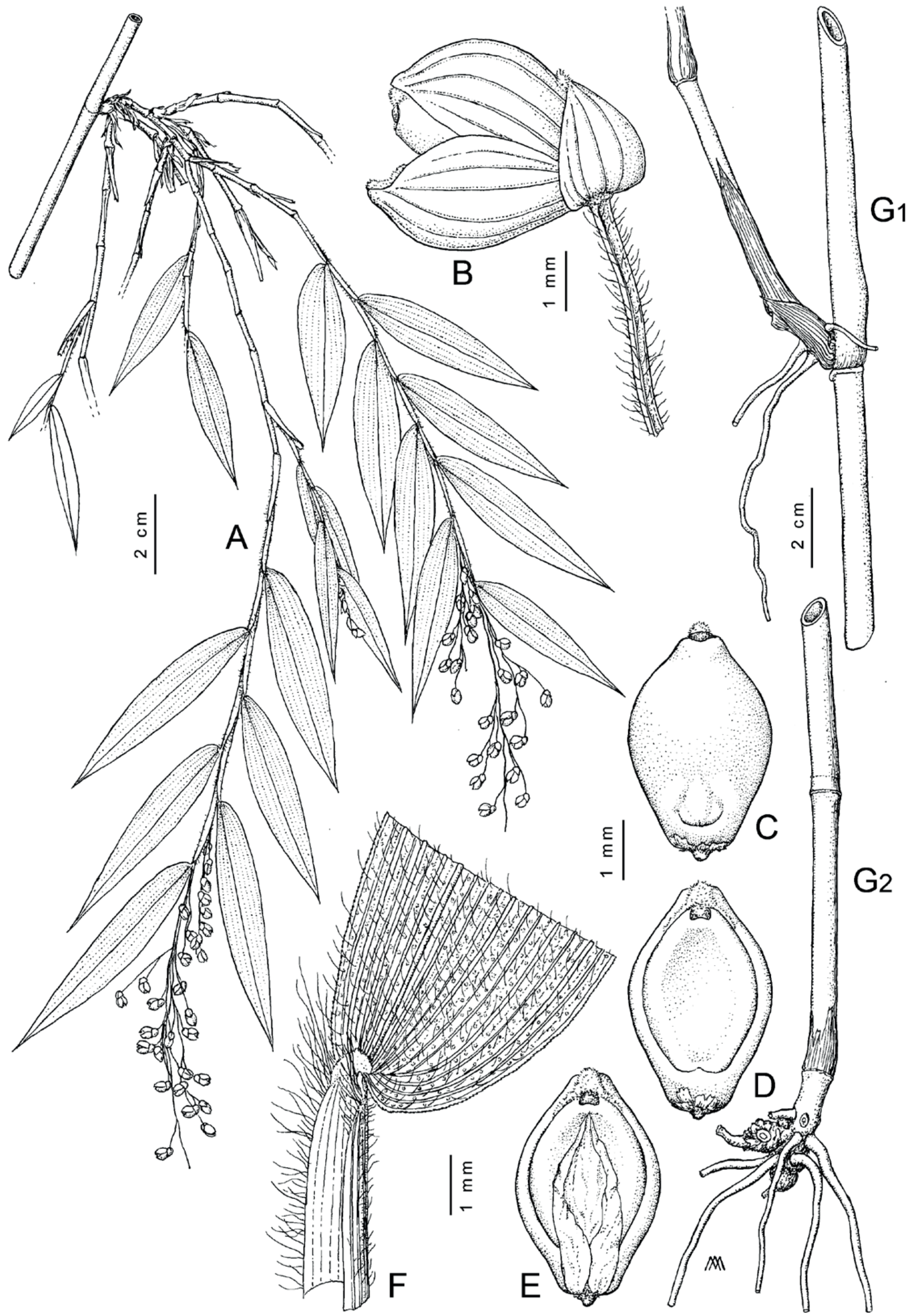

Figure 51. *Lasiacis velutina* Swallen: **A.** Habit with lateral procumbent fertile branches; **B**. Spikelet lateral view; **C.** Fertile upper floret dorsal view; **D**. Fertile upper floret ventral view without lower persistent palea; **E.** Fertile upper floret ventral view with lower persistent palea; **F.** Ligular area [A-F. from *P.C. Standley 26686* (MO)]; **G1**. Portion of the culm at medium length rooting at the nodes; **G2.** Culm towards the base. [G1-G2. from *G. Davidse & R.W. Pohl 2162* (MO)]. *A. Maury delineavit.*

Figure 52. *Lasiacis velutina* Swallen: general geographic distribution.

Ecology

Often in pine/oak montane forests, sprawling on other plants. Elevation from sea level (Honduras: Atlantida, *G. Davidse & R.W. Pohl 2188* (K, L, MO, NY, US) up to 1000-1100 m [Honduras: Morazán, *P.C. Standley 26686* (MO)].

Phenology

June through December, in southern America in February/March.

Remarks

Lasiacis velutina is distinguished by its pilose-velutinous pubescence, leaf blades subovate to ovate, small ligule, purple small globose spikelets, and open inflorescences. It is related to *L. ruscifolia* and for some characters such as open panicle, and dense purple spikelets reminds *L. nigra* Davidse.

I resurrect this taxon at the species level as originally described by Swallen (1955) not excluding a possible hybrid origin between *L. ruscifolia* and *L. nigra* hypothesized by Davidse (1978).

L. velutina is mainly distributed in Honduras, and in scattered areas in Colombia, Costa Rica, Ecuador, El Salvador and Venezuela. I traced an interesting record from Cuba [Pinar del Río, Mendoza, in forest at Río Cuyaguateje, 26 Jun. 1920, *E.L. Ekman 11490* (G)] referable to *L. velutina*, suggesting that this taxon deserves more attention in the field and in herbaria, because it is often confused with *L. ruscifolia*.

Selected specimens

COLOMBIA. Huila. Garzón, Vereda de las Quebraditas, 900 m, 21–26 Feb. 1947, *L.A. Bermudez 34933* (G).

COSTA RICA. **Guanacaste**. About 8 km due north of Liberia, 10°42'N, 85°27'W, 2 Aug. 1971, *W.C. Burger & Burger M. 7855* (NY).

ECUADOR. Manabí. s.l., 1897, *H.F.A. von Eggers 15553* (L, P).

EL SALVADOR. **Santa Ana**. Depto. Santa Ana, Chalchuapa, Cantón El Jute, A.N.P. La Magdalena, Sendero del Cerro Pelón al Sector El Tanque, -14.09297° -89.70224°, 11 Jul. 2012, *D. Rodriguez et al. 3300* (K, LAGU, MO).

HONDURAS. **Atlantida**. 9 km E of Tela, 10 m, 26 Jun. 1970, *G. Davidse & R.W. Pohl 2188* (K, L, MO, NY, US), **n = 18!** (as *L. ruscifolia*, Davidse 1978); **Copán**. 8 km de Santa Rosa de Copán entre El Portello y San Juan Opoa, 23 Sep. 1963, *A. Molina 12880* (US); **El Paraiso.** Matorrales húmedos-enguamilados entre Mata Indio y Lizapa, 25 Jul. 1951, *A. Molina 4051* (US); **Morazán**. Clara Creek, Zamorano Valley near Santa Inés, 23 Aug. 1946, *L.O. Williams & A. Molina 10407* (MO, US); Drainage of the Río Yeguare, 24 Jun. 1948, *S.F. Glassman 1732* (NY); Along Río Yeguare E of El Zamorano, Sep.-Dec. 1948, *P.C. Standley 12728* (NY); Márgenes de la quebrada de las Burras entre Suyapa y Tegucicalpa, 11 Dic. 1948, *A. Molina 1811* (US); Along Río Agua Amarilla, above El Jicarito, 900-1100 m, 2 Mar. 1949, *P.C. Standley 26686* (MO); El Zamorano, along road toward San Antonio de Oriente, 800-1000 m, 9 Aug. 1949, *P.C. Standley 22316* (P); Las Mesas, 800-900 m, 3 Sep. 1949, *P.C. Standley 23373* (P); Vicinity of El Zamorano, La Quince to El Jicarito, 800-850 m, 10 Sep. 1949, *P.C. Standley 23574* (P); Above Zamorano, near Río Agua Amarilla, 14 Sep. 1950, *P.C. Standley 26683* (BM); Cerro Majicoran, above Río de la Orilla, 16 Oct. 1949, *L.O. Williams 16928* (BM, MO); Río de la Orilla, vicinity of El Zamorano, 16 Oct. 1949, *P.C. Standley 24173* (NY, US); El Jicarito, above El Zamorano, Río Caparrosa, small vine, 900-1000 m, 1 Dec. 1949, *P.C. Standley 24859* (P); Río del Gallo, near El Jicarito, about 2 km from El Zamorano, 22 Oct. 1951, *J.R. Swallen 11008* (G, NY, P, US); Along Río Rancho Quemado, SE of Tegucicalpa, 20-25 km road to Sabana Grande, 9 Nov. 1966, *A. Molina 18631* (G, NY); Between El Zamorano and San Antonio de Oriente, brushy hillside which was originally pine forest, 1100 m, 21 Jun. 1970, *G. Davidse & R.W. Pohl 2162* (MO), **n = 18!** (as *L. ruscifolia* var. *velutina*, Davidse 1978); Quarry above El Zamorano, ca. 1000 m, in brush, to 4-5 m tall, 21 Nov. 1970, *G. Davidse & R.W. Pohl 12508* (MO); Quebrada detras de La Aldea de Suyapa, 950 m, 13 May 1983, *V.L. Ochoa 161* (MO); **Olancho**. Catamas, 11 Sep. 1991, *M. Chorley 170* (BM).

VENEZUELA. **Districto Federal**. Las Colinas de Sosa, Oct. 1939, *F. Tamayo 2010* (US, VEN); Cerro Naiguatá, arriba del pueblo de Naiguatá, Lomas de las Delicias, entre Quebrada de Basenilla y Quebrada Guayoyo, suroeste de Hacienda Cocuizal, 100-1300 m, 15-19 Nov. 1963, *J.A. Steyermark 92125* (US, VEN); **Guárico**. Sabanas de la Estación Biologica de Los Llanos, 10 km al sureste Calabozo, 8°52'N, 67°22'W, 200 m, 7 Aug. 1989, *F.O. Zuloaga & al. 4355* (US, VEN).

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REFERENCES

Acevedo-Rodríguez P. 2005. Vines and Climbing Plants of Puerto Rico and the Virgin Islands. Contributions from the United National Herbarium. 51: 1-483.

Acevedo-Rodríguez P, Strong MT. 2012. Catalogue of Seed Plants of the West Indies. Smithsonian Contributions to Botany. 98: 1-1192.

Adams CD. 1972. Flowering Plants of Jamaica. Pp.1-848. University of the West Indies, Mona, Jamaica.

Allan JA. 1957. The Grasses of Barbados. Pp. 26-27. Her Majesty's Stationery Office, London.

Alves da Silva G, Acioli dos Santos B, Alves MV, Costa Maia L. 2001. Arbuscular mycorrhiza in species of Commelinidae (Liliopsida) in the State of Pernambuco (Brazil). Acta Botánica Brasilica. 15(2): 155- 165.

Amshoff GJH, Henrard JTh. 1948. *Lasiacis* (Griseb.) Hitchc. In: Pulle A. (Ed.), Flora of Suriname (Netherlands Guyana), Vol. 1(1): 398-401. J.H. de Bussy Ltd., Amsterdam.

Arrieta Herrera Y, Peterson P.M. 2018. Grasses of Chihuahua, Mexico. Smithsonian Contributions to Botany 107: 1-380.

Bacon CD, Mora A, Wagner WL, Jaramillo CA. 2012. Testing geological models of evolution of the Isthmus of Panama in a phylogenetic framework. Botanical Journal of Linnaean Society. 171(1): 287-300. https://doi.10.1111/j.1095-8339.2012.01281.x

Boejharat VP. 2015. Preliminary study on the feasibility of developing bamboo products within the context of socio-economic and cultural reality in Kwamalasamutu. BSc Thesis. Faculty of Technology, Anton de Kom Universiteit van Suriname. Paramaribo, Suriname. Pp. 1-64.

Baldini RM. 2010. *Panicum maculatum* Aubl.: its type and the correct use of *Lasiacis maculata* (Aubl.) Urb. (Poaceae, Paniceae). Adansonia, sér. 3. 32(1): 109-119.

Baldini RM, Cota-Sánchez JH, Aedo C. 2021. Is the demise of plant taxonomy in sight? Maybe yes, maybe no… Webbia. 76(1): 3-10. doi:10.36253/jopt-10802.

Bebber DP, Carine MA, Wood JRI, Wortley AH, Harris DJ, Prance GT, Davidse G, Paige J, Pennington TD, Robson NKB, Scotland RW. 2010. Herbaria are a major frontier for species discovery. PNAS. 107(51): 22169-22171. doi:10.1073/pnas.1011841108.

Beentje H. 2010. The Kew Plant Glossary, an illustrated dictionary of plants terms. Royal Botanic Gardens, Kew.

Beetle AA. 1977. Noteworthy grasses from Mexico V. Phytologia. 37(4): 317-407.

Bennet BC. 1990. Useful Plants of Amazonian Ecuador. 5th Progress Report 15 April 1990 – 15 October 1990. US Agency for International Development. Institute of Economic Botany, New York Botanical Garden Pp. 1-349.

Boldingh I. 1909. The Flora of the Dutch West Indian Islands St. Eustatius, Saba and St. Martin. 1. E.J. Brill, Leiden.

Bono G. 1996. Flora y Vegetacion Del Estado Táchira. Venezuela. Museo Regionale di Scienze Naturali, Monografie. XX: 9-949. [*Lasiacis* (Griseb.) Hitchc.: 570).

Bono G. 2010. Catálogo de la Flora y Vegetacion de los Valles de la vertiente occidental de los Andes de la Cordillera de Mérida. Centro Studi Erbario Tropicale. Publ. 116: 1-489. Firenze.

Bosser J, Florens D. 1999. *Pseudolasiacis* (A.Camus) A.Camus (Poaceae) à Madagascar, aux Comores et aux Mascareignes. Adansonia, sér. 3. 21(2): 231-237.

Bouchenak-Khelladi Y, Verboom GA, Savolainen V, Hodkinson TR. 2010. Biogeography of the grasses (Poaceae): A phylogenetic approach to reveal evolutionary history in geographical space and geological time. Botanical Journal of the Linnean Society. 162: 543-557. doi:10.1111/j.1095-8339.2010.01041.x

Burke SV, Wysocki WP, Zuloaga FO, Craine JM, Pires CJ, Edger PP, Mayfield-Jones D, Clark LG, Kelchner SA, Suvall MR. 2016. Evolutionary relantioships in Panicoid grasses based on plastome phylogenomics (Panicoideae; Poaceae). BMC Plant Biology. 16: 140. https://doi.org/101186/s12870-016-0823-3

Bussmann RW. 2003. The vegetation of Reserva Biológica San Francisco, Zamora-Chinchipe, Southern Ecuador – a phytosociological synthesis. Lyonia. 3(2): 145-254.

Butzin F. 1970a. Die Blattnervatur der Paniceae in ihrer Bedeutung für die systematische Gliederung dieser Tribus. Willdenowia. 6(1): 167-178.

Butzin F. 1970b. Die systematische Gliederung der Paniceae. Willdenowia. 6(1): 179-192.

Camus A. 1926. *Panicum* nouveaux de la section *Pseudolasiacis* A.Camus. Bulletin de la Société Botanique de France. 73: 974-977.

Cannoni G. 2013. Il genere *Lasiacis* (Griseb.) Hitchc. (Poaceae, Paniceae): preliminary considerations on the morphology and distribution. MSc thesis in Natural Science, University of Florence (Italy), Academic Year 2012-2013. (in Italian).

Catasús Guerra L. 2012a. *Lasiacis* (Griseb.) Hitchc. In: Greuter W, Rankin Rodríguez R. (Eds.), Flora de Cuba 17A: Poaceae 1 (texto): 231-238. Koeltz, Königstein, Germany.

Catasús Guerra L. 2012b. *Lasiacis* (Griseb.) Hitchc. In: Greuter W, Rankin Rodríguez R. (Eds.), Flora de Cuba 17B: Poaceae 1 (Láminas): 306-317. Koeltz, Königstein, Germany.

Chase A. 1911. Notes of Genera of Paniceae IV. Proceedings of the Biological Society of Washington. 24: 103-160.

Cialdella AM., Vega AS. 1996. Estudios sobre la variación estructural de las espiguillas en géneros de la Tribu Paniceae (Poaceae). Darwiniana. 34(1-4): 173-182.

Clayton WD, Renvoize SA. 1986. Genera Graminum. Grasses of the World. Kew Bulletin Additional Series XIII: 1-389. Royal Botanic Gardens, Kew, UK.

Clifford HT, Bostock PD. 2007. Etymological Dictionary of Grasses. Springer-Verlag, Berlin, Heidelberg and New York.

Cope TA. 2005. The chorology of Central and South American grasses. Kew Bulletin. 60: 515-545.

Correa MD, Galdames C, de Stapf S.M. 2004. Catálogo de las Plantas Vasculares de Panamá: 227. Quebedor World Bogotá, Colombia.

Croat TB. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, California. Pp. 1-943.

D'Arcy WG. 1987. Flora of Panama. Check List Part II: Index. Pp. 1-670. Missouri Botanical Garden, St. Louis. [*Lasiacis* (Griseb.) Hitchc.: 340-341].

Davidse G. 1972. A systematic study of the genus *Lasiacis* (Gramineae, Panicoideae). Retrospective Theses and Dissertations. Iowa State University, Ames. Pp. 1-96. https://lib.dr.iastate.edu/rtd/4731

Davidse G. 1974. A new species of *Lasiacis* (Gramineae). Phytologia. 29: 152-153.

Davidse G. 1977. New Taxa and Combinations in the Genus *Lasiacis* (Gramineae). Annals of the Missouri Botanical Garden. 64(2): 374-375.

Davidse G. 1978. A systematic study of the genus *Lasiacis* (Gramineae: Paniceae). Annals of the Missouri Botanical Garden. 65: 1133-1254.

Davidse G. 1985. The Phytogeographic Relationships of the Panamanian Grasses. In: D'Arcy WG, Correa MD. (Eds.), The Botany and Natural History of Panama. Pp. 13-24. Missouri Botanical Garden, Saint Louis.

Davidse G. 1987. Fruit Dispersal in the Poaceae. In: Soderstrom TR, Hilu KW, Campbell CS, Barkworth ME. (Eds.), Grass Systematics and Evolution. Pp. 143-155. Smithsonian Institution Press, Washington, D.C., London.

Davidse G. 1994. *Lasiacis* (Griseb.) Hitchc. In: Davidse G, Sousa MS, Chater AO. (Eds.), Flora Mesoamericana. Vol. 6. Alismataceae a Cyperaceae. Universidad Nacional Autónoma de México.

Davidse G. 2001. *Lasiacis* (Griseb.) Hitchc. In: Stevens WD, Ulloa Ulloa C, Pool A, Montiel OM (Eds.), Flora de Nicaragua. Angiospermas (Pandanaceae-Zygophyllaceae). 85(3): 2064-2069. Missouri Botanical Garden Press.

Davidse G. 2003. *Lasiacis* (Griseb.) Hitchc. In: Backworth ME, Capels KM, Long S, Piep MB. (Eds.), Flora of North America, North Mexico [Magnoliophyta: Commelinidae (in Part): Poaceae]. Vol. 25(2): 388-389. New York, Oxford University Press.

Davidse G. 2004. *Lasiacis* (Griseb.) Hitchc. In: Berry PE, Yatskievych K, Holst BK (Eds.), Flora of the Venezuelan Guayana. Poaceae-Rubiaceae. Vol. 8: 137-143. Missouri Botanical Garden Press.

Davidse G. 2007. *Lasiacis* (Griseb.) Hitchc. In: Barkworth ME, Anderton LK, Capels KM, Long S, Piep MB. (Eds.), Manual of Grasses for North America: 275-276. Intermountain Herbarium and Utah State University Press, Logan, Utah.

Davidse G. 2008. Poaceae. In: Daly DC, Silveira M. (Eds.), First Catalogue of the Flora of Acre, Brasil. Pp. 1-555. EDUFAC, Rio Branco, Acre. [*Lasiacis* (Griseb.) Hitchc.: 306].

Davidse G, Morton E. 1973. Bird-mediated Fruit Dispersal in the Tropical Grass Genus *Lasiacis* (Gramineae: Paniceae). Biotropica. 5(3): 162-167.

Davidse G, Judziewicz EJ, Zuloaga FO. 2007. Poaceae. In: Funk V, Hollowell T, Berry P, Kelloff C, Alexander SN. (Eds.), Checklist of the Plants of the Guiana Shiled (Venezuela: Amazonas, Bolívar. Delta Amacuro; Guyana, Surinam, French Guiana. Contributions from the United States National Herbarium. 55: 149-172.

Dávila P, Mejia-Saulés MT, Soriano-Martínez AM, Herrera-Arrieta Y. 2018. Conocimiento taxonómico de la familia Poaceae en México. Botanical Sciences. 96(3): 462-514. https://doi.org/10.17129/botsci.1894

Davis PH, Heywood VH. 1963. Principes of angiosperm taxonomy. Van Norstrand, New York, xx + 556 pp.

Dórea MC, Santos DWJ, Oliveira RP, Funch LS, Santos FAR. 2018. Reproductive traits related to anemophily and insect visitors in two species of Poaceae from the Brazilian Atlantic rainforest. Brazilian Journal of Botany. 41: 425-434.

Dorr LJ. 2014. Flora of Guaramacal (Venezuela): Monocotyledons. Smithsonian Contributions to Botany. 100: v + xii, 1:287.

Doyle JJ, Flagel LE, Paterson AH, Rapp RA, Soltis DE, Soltis PS, Wendel JF. 2008. Evolutionary Genetics of Genome Merger and Doubling in Plants. Annual Review of Genetics. 42: 21.1-21.19. https://doi.org/10.1146/annurev.genet.42.110807.091524

Ebach MC, Valdecasas AG, Wheeler QD. 2011. Impediments to taxonomy and users of taxonomy: accessibility and impact evaluation. Cladistics. 27: 550-557. https://doi.org/10.1111/j.1096-0031.2011.00348.x

Foster RC. 1966. Studies in the Flora of Bolivia. IV. Gramineae. Rhodora. 68(774): 223-358.

Fournet J. 1978. Flore illustrée des phanérogames de Guadeloupe et de Martinique: 151-153. Institut National de la Reserche Agronomique, Paris.

Franisco-Ortega J, Santiago-Valentín E, Acevedo-Rodríguez P, Lewis C, Pipoly III J, Meerow AW, Maunder M. 2007. Seed Plant Genera Endemic to the Caribbean Island Biodiversity Hotspot: A Review and a Molecular Phylogenetic Perspective. The Botanical Review. 73(3): 183-234.

Furuya SN, Castillo-Suárez A, Huber O. 2019. Catálogo y análisis florístico de las sábanas en el sector Puerto Ayacucho del Estado Amazonas, Guayana Venezolana. Acta Botánica Venezuelica. 42(1-2): 31-113.

Gagné RJ. 1969. A new genus and two new species of Cecidomyiidae associated with *Pariana* ssp.

(Gramineae) in South America. Proceedings of the Entomological Society of Washington. 71(1): 108-111.

Gallaher TJ, Adams DC, Attigala L, Burke SV, Craine JM, Duvall MR, Klahs PC, Sherratt E, Wysocky WP, Clark LG. 2019. Leaf shape and size track habitat transitions across forest-grassland boundaries in the grass family (Poaceae). Evolution. 73(5): 927-946. https://doi.org/10.1111/evo.13722

Gallaher TJ, Peterson PM, Soreng RJ, Zuloaga FO, De-Zhu Li, Clark LG, Tyrrell CD, Welker CAD, Kellogg EA, Teisher JK. 2022. Grasses through space and time: An overview of the biogeographical and macroevolutionary history of Poaceae. Journal of Systematics and Evolution. 60(3): 522-569. https://doi.org/10.111/jse.12857

Gentry AH. 1982. Neotropical Floristic Diversity: Phytogeographical Connections between Central and South America, Pleistocene Climatic Fluctuations, or an Accident of the Andean Orogeny? Annals of the Missouri Botanical Garden. 69: 557-593. https://www.jstor.org/stable/2399084

GBIF (continuously updated). Global Biodiversity Information Facility. https://www.gbif.org/ (accessed 15 Mar 2025).

Gibson DJ. 2009. Grasses and Grassland Ecology. Oxford University Press.

Graham A. 2010. Late Cretaceous and Cenozoic History of Latin America Vegetation and Terrestrial Environments. Monographs in Systematics Botany from the Missouri Botanical Garden 113: 1-617.

Graham A. 2011. A Natural History of the New World. The Ecology and Evolution of Plants in the Americas. Pp. 1-387. The University of Chicago Press, Chicago & London.

Graham A. 2018. Land Bridges. Ancient Environments, Plant Migrations, and New World Connections. Pp. 1-310. The University of Chicago Press, Chicago & London.

Santos GCA, Sano TP. 2001. *Lasiacis* (Griseb.) Hitchc. In: Wanderley MGL, Sheperd GJ, Giulietti AM. (Eds.), Flora Fanerogâmica do Estado de São Paulo. Poaceae. Vol. 1: 163-164. Editorial Hucitec, São Paulo, Brasil.

Giraldo-Cañas D. 2010. Distribución e invasión de Gramíneas C_3 y C_4 (Poaceae) en un gradiente altitudinal de los Andes de Colombia. Caldasia. 32(1): 65-86.

Giraldo-Cañas D**.** 2011. Checklist of the family Poaceae from Colombia. Darwiniana. 49(2): 139-247.

Giussani LM, Cota-Sánchez JH, Zuloaga FO, Kellogg EA. 2001. A molecular phylogeny of the grass subfamily Panicoideae (Poaceae) shows multiple origins of C_4 photosynthesis. American Journal of Botany. 88(11): 1993-2012.

Gorneau JA, Ausich WI, Bertolino S, Bik H, Daly M, Demissew S, Donoso DA, Folk R, Freire-Fierro A, Ghanzafar SA, Grace OM, Ai-Qun Hu, Kulkarni S, Lichter-Marck IH, Lohmann LG, Malumbres-Olarte J, Muthama Muasya A, Pérez-GonzálezBulletin of the Society of Systematic Biologists A, Singh Y, Simiscalchi CM, Specht CD, Stigall AL, Tank DC, Walker LA, Wright DF, Zamani A, Esposito LA. 2022. Framing the future for taxonomic monography: Improving recognition, support, and access. Bulletin of the Society of Systematic Biologists, Jan. 2022. https://doi.org/10.18061/bssb.viii.8328

Gould FW, Shaw RB. 1983. Grass Systematics. 2nd Edition. Texas & A&M Univeristy Press.

Gould FW, Soderstrom TR. 1967. Chromosome numbers of Tropical American Grasses. American Journal of Botany. 54(6): 676-683.

Gould FW, Soderstrom TR. 1970. Chromosome numbers of some Mexican and Colombian grasses. Canadian Journal of Botany. 48: 1633-1639.

Gould FW, Moran R. 1981. The Grasses of Baja California, Mexico. San Diego Society of Natural History Memoirs. 12: 1-140.

Grisebach AHR. 1864. Flora of the British West Indian Islands. Lovell Reeve & Co. London.

Hackel J, Vorontsova MS, Nanjarisoa OP, Hall RC, Razanatsoa J, Malakasi P, Besnard G. 2018. Grass diversification in Madagascar: In situ radiation of two large C_3 shade clades and support for a Miocene to Pliocene origin of C_4 grassy biomes. Journal fo Biogeography. 45: 750-761. Doi:10.1111/jbi.13147.

Herrera Arrieta Y, Peterson PM, Cortés Ortiz A. 2010. Gramíneas de Zacatecas, México. Sida Botanical Miscellany 32: 1-239.

Heywood V. 2001. Floristics and monography – an uncertain future? Taxon. 50: 361-380.

Hilu KW. 2004. Phylogenetics and chromosomal evolution in the Poaceae (grasses). Australian Journal of Botany. 52: 13-22.

Hitchcock AS. 1908. Types of American Grasses: a study of the American species of grasses described by Linnaeus, Gronovius, Sloane, Swartz, and Michaux. Contributions from the U.S. National Herbarium. 12(3): 113-157.

Hitchcock AS. 1909. Catalogue of the Grasses of Cuba. Contributions from the U.S. National Herbarium. 12(6): 183-258.

Hitchcock AS. 1910. The North American Species of *Panicum*. Contributions from the U.S. National Herbarium. 15: 1-396.

Hitchcock AS. 1911. Additions to the Grasses of Cuba. Botanical Gazette. 51(4): 300-302.
Hitchcock AS. 1913. Mexican grasses in the United States National Herbarium. Contributions from the U.S. National Herbarium. 17(3): 181-389.
Hitchcock AS. 1919. A peculiar species of *Lasiacis*. Journal of the Washington Academy of Sciences. 9(2): 35-38.
Hitchcock AS. 1920. The North American Species of *Lasiacis*. In: Hitchcock AS, Chase A. (Eds.), Revisions of American Grasses. Contributions from the U.S. National Herbarium. 22(1): 13-31.
Hitchcock AS. 1922. Grasses of British Guiana. Contributions from the U.S. National Herbarium. 22(6): 439-514.
Hitchcock AS. 1927a. The Grasses of Ecuador, Peru, and Bolivia. Contributions from the U.S. National Herbarium. 24(8): 291- 556.
Hitchcock AS. 1927b. New species of grasses from Central America. Proceedings of the Biological Society of Washington. 40: 79-88.
Hitchcock AS. 1930. The grasses of Central America. Contributions from the U.S. National Herbarium. 24(9): 557-762.
Hitchcock AS. 1936. Manual of the grasses of the West Indies. USDA Miscellaneous Publications. 243: 1-439. Washington D.C., USA.
Hitchcock AS, Chase A. 1910. The North American species of *Panicum*. Contributions from the U.S. National Herbarium. 15: 1-396.
Hitchcock AS., Chase A. 1917. Hitchcock AS, Chase A. Grasses of the West Indies. Contributions of the U.S. National Herbarium. 18(7): 335-339.
Hitchcock AS, Chase A. 1950. Manual of the Grasses of the United States. 2nd revised Ed. by A. Chase. USDA Miscellaneous Publication No. 200, Washington D.C.
Hodkinson TR. 2018. Evolution and Taxonomy of the grasses (Poaceae): A model family for the study of species-rich groups. Annual Plant Reviews. 1: 1-39. https://doi.org/10.1002/9781119312994.apr0622
Hokche O, Berry PE, Huber O. 2008. Nuevo Catálogo de la Flora Vascular de Venezuela. Pp. 1-859. Fundación Istituto Botánico de Venezuela Dr. Tobias Lasser, Caracas.
Hoyos JF. 1985. Flora de la Isla Margarita. Venezuela. Sociedad y Foundacion La Salle de Ciencias Naturales. Monografia. N. 34: 11-927.
Hollowell T, Gillespie LJ, Funk VA, Kelloff CL. 2003. Smithsonian Plant Collections, Guyana: 1989- 1991, Lynn Gillespie. Contributions from the United States National Herbarium. 44: 1-104.
Hollowell T, McDowell T, Funk VA, Kelloff CL, Gopaul D. 2004. Smithsonian Plant Collections, Guyana: 1990-1991, Tim McDowell. Contributions from the United States National Herbarium. 50: 1-150.
Holmgren PK, Keuken W, Schofield EK. (1900-). Index Herbariorum. The Herbaria of the World. The New York Botanical Garden, The Bronx, New York. Continuously published online: https://sweetgum.nybg.org/science/ih/
Hoshikawa K. 1969. Underground Organs of the Seedlings and the Systematics of Gramineae. Botanical Gazette. 130(3): 192-203.
Howard RA. 1979. Flora of the Lesser Antilles. Monocotyledonae. Vol. 3: 165-169. Arnold Arboretum, Harvard University, Jamaica Plain, Massachuttes.
Hunziker JH, Stebbins Ledyard G. 1987. Chromosomal Evolution in the Gramineae. In: Soderstrom TR, Hilu KW, Campbell CS, Barkworth ME. (Eds.), Grass Systematics and Evolution. Pp. 179-187. Smithsonian Institution Press, Washington, D.C., London.
Ibáñez A, Castroviejo S, Fernández Alonso JF, Correa MD. 2005. V. Catálogo de la Flora de la Región de Bahia Honda (Veraguas, Panamá): 177-362. In: Castroviejo S, Ibáñez A. (Eds.), Estudios sobre la Biodiversidad de la Región de Bahía Honda (Veraguas, Panamá). Biblioteca de Ciencias 20: 1-835. Consejo Superior de Investigaciones Científicas, Instituto de España, Real Academia de Ciencias Exactas, Físicas y Naturales. Madrid.
Ibrahim DG, Burke T, Ripley BS, Osborne CP. 2009. A molecular phylogeny of the genus *Alloteropsis* (Panicoideae, Poaceae) suggests an evolutionary reversion from C_4 to C_3 photosynthesis. Annals of Botany. 103: 127-136. https://doi.org/10.1093/aob/mcn204
Isely D. 1972. The disappearance. Taxon. 21(1): 3-12.
IPNI. 2025. International Plant Names Index. The Royal Botanic Gardens, Kew, Harvard University Herbaria & Libraries and Australian National Herbarium [Retrieved January 2025].
Jarvis C. 2007. Order out of Chaos. Linnaean plant names and their types. The Linnean Society of London and the Natural History Museum, London.
Judziewicz EJ. 1990. *Lasiacis* (Griseb.) Hitchc. In: Görts-Rijn ARA. (Ed.), Flora of the Guianas. Series A: Phanerogams. 187. Poaceae (by EJ Judziewicz): 303-309. Koeltz, Königstein, Germany.
Judziewicz EJ. 1997. *Lasiacis* (Griseb.) Hitchc. In: Mori SA, Cremers G, Gracie C, de Granville J-J, Hoff M, Mitchell JD. (Eds.), Guide to the Vascular Plants of the Central Guiana. Part 1. Memoirs of the New York Botanical Garden. 76(1): 350.
Kirby MX, MacFadden B. 2005. Was southern Central America an archipelago or a peninsula in the middle Miocene? A test using land-mammal body size. Pal-

aeogeography, Palaeoclimatology, Palaeoecology 228: 193-202. doi:10.1016/j.palaeo.2005.06.002

Kellogg EA. 2015. Flowering Plants Monocots: Poaceae. In: Kubitzki K. (Ed.), The Families and Genera of Vascular Plants. Vol. XIII. Pp. 1-416. Springer Verlag, Heidelberg.

Killeen TJ. 1990. The Grasses of Chiquitania, Santa Cruz, Bolivia. Annals of the Missouri Botanical Garden. 77(1): 125-201. http://www.jstor.org/stable/2399632

Kunth C-S. 1835. Distribution Méthodique de la famille Des Graminées 2. Librairie-Gide, Paris.

Lagomarsino LP, Frost LA. 2020. The Central Role of Taxonomy in the Study of Neotropical Biodiversity. Annals of the Missouri Botanical Garden. 105: 405-421. doi : 10.3417/2020601

Leigh EG, O'Dea A, Vermeij GJ. 2014. Historical biogeography of the Isthmus of Panama. Biological Reviews. 89 : 148-172. Doi : 10.111/brv.12048

Lemée A. 1955. Flore de la Guyane française. Ptéridophytes à Droséracées. 1: 1-701. Le Chevalier, Paris.

Lentz DL. 1986. Ethnobotany of Jicaque of Honduras. Economic Botany. 40: 210-218.

Lindeman JC, Stoffers AL. 1963. Gramineae. In: Stoffers AL. (Ed.), Flora of the Netherlands Antilles. Pp. 121-203. Utrecht.

Lipp FJ. 1971. Ethnobotany of the Chinantec Indians, Oaxaca, Mexico. Economic Botany 25(3): 234-244.

Löbl I, Klausnitzer B, Hartmann M, Krell F-T. 2023. The Silent Extinction of Species and Taxonomists-An Appeal to Science Policymakers and Legislators. Diversity. 15(10), 1053, doi.org/10.3390/d15101053

McNeill J. 2014. Holotype specimens and type citations: General issues. Taxon. 63(5): 1112-1113.

McVaugh R. 1983. *Lasiacis* (Griseb.) Hitchc. In: Anderson WR. (Ed.), Flora Novo-Galiciana: A Descriptive Account of the Vascular Plants of Western Mexico. Gramineae. Vol. 14: 206-210. The University of Michigan Press, Ann Harbour.

Menjívar Cruz J.E., Baldini R.M., Davidse G, & Peterson P.M. 2021. El Salvador Grasses: An updated catalogue and nomenclator. Phytoneuron. 2021-22: 1-131.

Minelli A. 1993. Biological Systematics. The State of the Art. Chapman & Hall, London.

Moldenke HN. 1944. A Contribution to Our Knowledge of the Wild and Cultivated Flora of Florida I. American Midland Naturalist. 32(3): 529-590.

Morales JF. 2003. *Lasiacis* (Griseb.) Hitchc. In: Hammel BE, Grayum MH, Herrera C, Zamora N. (Eds.), Manual de plantas de Costa Rica. Gimnospermas y Monocotiledoneas (Agavaceae-Musaceae). Vol 2: 711-716. Missouri Botanical Garden, St. Louis, MO, USA.

Morrone O, Zuloaga FO. 1994. *Lasiacis* (Griseb.) Hitchc. In: Gramineae V. Panicoideae-Paniceae: *Acroceras* Stapf – *Panicum* L. Flora del Paraguay. 23: 187-193. Conservatoire et Jardin botaniques de la Ville de Genève.

Morrone O, Zuloaga FO. 2012. *Lasiacis* (Griseb.) Hitchc. In: Zuloaga FO, Rúgolo de Agrasar ZE, Anton AM. (Eds.), Flora Argentina. Monocotyledonae: Poaceae: Aristidoideae a Pharoideae. Vol. 3(1): 332-334. Cordoba, Argentina.

Morrone O, Denham SS, Aliscioni SS, Zuloaga FO. 2008. *Parodiophyllochloa*, a New Genus Segregated from *Panicum* (Paniceae, Poaceae) Based on Morphological and Molecular Data. Systematic Botany. 33(1): 66-76.

Morrone O, Zuloaga FO, Longhi-Wagner HM, Izaguirre P, Beyhaut R, Cialdella AM, Giussani L, Denham SS, Guglieri A, Boldrini I, Zanín A, Salariato D, De Gennaro D. 2008. Poaceae. In: Zuloaga FO, Morrone O, Belgrano MJ. (Eds.), Caálogo de las Plantas Vasculares del Cono Sur (Argentina, Sur de Brasil, Chile, Paraguay y Uruguay). Vol. 1. Monographs in Systematic Botany from the Missouri Botanical Garden. 107: 1-983.

Morrone O, Aagesen L, Scataglini MA, Salariato DL, Denham SS, Chemisquy MA, Sede SM, Giussani LM., Kellogg EA, Zuloaga FO. 2012. Phylogeny of the Paniceae (Poaceae: Panicoideae): integrating plastid DNA sequences and morphology into a new classification. Cladistics. 28: 333-356. https://doi.org/10.1111/j.1096-0031.2011.00384x

Morrone JJ, Ebacj MC. 2022. Toward a terrestrial biogeographical regionalisation of the world: historical notes, characterisation and area nomenclature. Australian Systematic Botany. 35(3): 187224. https://doi.org/10.1071/SB22002

Nash GV. 1908. Two new grasses from the West Indies. Bulletin of the Torrey Botanical Club. 35(6): 301-303.

Nash GV. 1913. Two new American Grasses. Torreya. 13(12): 273-274.

Nash GV. 1931. Poaceae. In: Hitchcock AS, Chase A, Swallen JR. (Eds.), North American Flora. 17(4): 294-300.

Nicora EG, Rúgolo de Agrasar ZE. 1987. Los géneros de Gramíneas de América Austral. E. hemisferio sur S.A. Buenos Aires.

Nuñez O. 1952. Investigaciones cariosistematicas en Las Gramineas Argentinas de la Tribu «Paniceae». Revista Facultad Agronomia, Eva Peron. (3ª ép.) 28(2): 229-256.

Palacios RA. 1968. Variaciones en la estructura de las espiguillas en algunas especies argentinas de *Pani-*

cum. Boletín de la Sociedad Argentina de Botánica.12: 38-43.

Pimm SL, Lawton JH. 1998. Planning for biodiversity. Science. 279: 2068-2069.

Pinto-Escobar P. 1966. Gramineae. Catálogo ilustrado de las plantas de Cundinamarca. Instituto de Ciencias Naturales, Universidad Nacional, Bogotá. Pp. 11-78.

Pohl RW. 1980. Family #15. Gramineae. In Burger W. (Ed.) Flora Costaricensis. Fieldiana: Botany. 15: 1-608.

Pott A, Pott VJ. 2021. Flora of Pantanal. Pp. 39-228. In: Damasceno-Junior GA, Pott A. (Eds.), Flora and Vegetation of Pantanal. Springer Nature, Switzerland. https://doi.org/10.1007/978-3-030-83375-6

POWO. 2025 (continuously updated). Plants of the Workd Online. Kew: Royal Botanic Gardens. https://powo.science.kew.org/ (accessed 15 Mar. 2025).

Proctor GR. 2012. Flora of the Cayman Islands. Pp. 7-724. 2nd Ed. Royal Botanic Gardens, Kew Publishing.

Purificaçao KN, Pascotto MC, Pedroni F, JMN Pereira, Lima NA. 2014. Interactions between frugivorous birds and plants in savanna and forest formations of the Cerrado. Biota Neotropica. 14(4): e20140068, 2014. https://doi.org/10.1590/1676-06032014006814

Rebman JP, Gibson J, Rich K. 2016. Annotated Check-List of the Vascular Plants of Baja California, Mexico. Proceedings of the San Diego Society of Natural History. 45: 1-353.

Quattrocchi U 2006. CRC World Dictionary of Grasses. Vol. 2 E-O: 1180-1184. Taylor & Francis, London.

Reeder JR. 1967. Notes on Mexican grasses VI. Miscellaneous chromosome numbers. Bulletin of the Torrey Botanical Club. 94(1): 1-17.

Reeder JR. 1968. Notes on Mexican grasses VIII. Miscellaneous chromosome numbers - 2. Bulletin of the Torrey Botanical Club. 95(1): 69-86.

Reeves RD, Baker AJM, Becquer T, Echevarria G, Miranda ZJG. 2007. The flora and biogeochemistry of the ultramafic soils of Goiás state, Brazil. Plant Soil. 293: 107-119.

Renvoize SA. 1984. The Grasses of Bahia. Pp. 113-114. Royal Botanic Gardens, Kew.

Renvoize SA. 1998. Gramineas de Bolivia. Pp. 408-412. The Royal Botanic Gardens, Kew.

Renvoize S, Vega AS, Rúgolo Agrasar ZE. 2006. *Lasiacis* (Griseb.) Hitchc. In: Harling G, Persson C. (Eds.), Flora of Ecuador. 241(3). Gramineae (part 3). Subfam. Panicoideae. Vol. 78: 41-47. Elanders Berlings, Malmö, Sweden.

Rodríguez EF, Vásquez R, Rojas R, Calatayud G, León B, Campos J. 2006. Nuevas adiciones de angiospermas a la Flora del Perú. Revesta Peruviana de Biológia. 13(1): 129-138.

Rogers G, Holder A. 1999. The grasses of Barbados (Poaceae). SIDA, Botanical Miscellany. 17: 34-35.

Roig y Mesa JT. 1963. Diccionario botánico de nombres vulgares cubanos. Ed. 3. Santiago de Las Vegas.

Roys RL. 1931. The Ethonobotany of Maya. Tulane University Middle American Research Series, Publication No. 2. New Orleans.

Saarela JM, Burke SV, Wysocki WP, Barrett MD, Clark LG, Craine JM, Peterson PM, Soreng RJ, Vorontsova MS, Duvall MR. 2018. A 250 plastome phylogeny of the grass family (Poaceae): topological support inder different data partitions. PeerJ. 6: e4299. https://doi.org/10.7717/peerj.4299

Sánchez-Ken JG. 2019. Riqueza de especies, clasificación y listado de las gramineas (Poaceae) de México. Acta Botanica Mexicana. 126: e1379. https://doi.org/10.21829/abm126.2019.1379

Saunders ME. 2017. Insect pollinators collect pollen from wind-pollinated plants: implications for pollination ecology and sustainable agriculture. Insect Conservation and Diversity. 11: 13-31. https://doi.org/10.1111/icad.12243

Schipp WA. 1933 [-1934]. Flora of British Honduras. Price List of Seeds Herbarium Material. Stann Creek, British Honduras.

Seres A, Ramírez N. 1995. Biologia floral y polinizacion de algunas Monocotiledoneas de un bosque nublado venezolano. Annals of the Missouri Botanical Garden. 82: 61-81.

Serna AE, López-Ferrari AR. 2000. *Lasiacis* (Griseb.) Hitchc. In: Serna AE, López-Ferrari AR (Eds.), Las Monocotiledónes mexicanas. Una Sinopsis Florística. 1. Lista de Referencia. Partes IX a XI. Pandanaceae a Zosteraceae. Pp. 114-116. Consejo Nacional de la Flora de México, A.C.

Serrano M, Terán J. 1998 [2000]. Identificaión de especies vegetales en Chuquisaca: teoría, prática y resultados. Pp. 1-129. Plan Agroforestal de Chuquisaca. Intercooperación, Fundación Ceibo, Sucre.

Smith LB, Wasshausen DR, Klein RM. 1982. *Lasiacis* (Griseb.) Hitchc. In: Reitz R. (Ed.), Flora Ilustrada Catarinense. Gramíneas. 45. *Deschampsia* até 84. *Pseudechinolaena*. Pp. 626-633. Santa Catarina, Brasil.

Smith ML, Hedges SB, Buck W, Hemphill, Inchaustegui S, Ivie MA, Martina D, Maunder M, Francisco-Ortega j. 2004. Caribbean Islands. Pp. 122-118. In: Mittermeier RA, Gil RR, Hoffman M, Pilgrim J, Brooks T, Mittermeier CG, Lamoreux J, da Fonseca GAB. (Eds.), Hotspots revisited: Earth's biologically richest and most threatened terrestrial ecoregions. CEMEX, Mexico D.F.

Snow DW. 1981. Tropical Frugivorous Birds and Their Food Plants: A World Survey. Biotropica 13(1): 1-14.

Soderstrom TR, Calderón CE. 1971. Insect pollination in tropical rain forest grasses. Biotropica. 3: 1-16.

Soreng R.J., Peterson P.M., Romaschenko K., Davidse G., Zuloaga F.O., Judziewicz E.J., Filgueiras T.S., Davis J.I. & Morrone O. 2015. A worldwide phylogenetic classification of the Poaceae (Gramineae). Journal of Systematics and Evolution. 53(2): 117-137. https://doi.org/10.1111/jse.12150

Soreng R.J., Peterson P.M., Romaschenko K., Davidse G., Teisher J.K., Clark L.G., Barberá P., Gillespie L.J. & Zuloaga F.O. 2017. A worldwide phylogenetic classification of the Poaceae (Gramineae) II: An update and a comparison of two 2015 classifications. Journal of Systematics and Evolution. 55(4): 259-290. https://doi.org/10.1111/jse.12262

Soreng R.J., Peterson P.M., Zuloaga F.O., Romaschenko K., Clark L.G., Teisher J.K., Gillepspie L.J., Barberá P., Welker C.A.D., Kellogg E.A., De-Zhu Li, Davidse G. 2022. A worldwide phylogenetic classification of the Poaceae (Gramineae) III: An update. Journal of Systematics and Evolution. 60(3): 476-521. https://doi.org/10.1111/jse.12847

Standley PC. 1930. Flora of Yucatan. Field Museum of Natural History Publication 279, Botany series. Vol. III(3). Chicago.

Standley PC. 1937. Flora of Costa Rica. Part I: 79-80. Field Museum of Natural History, Vol. XVIII, Botanical Series. Chicago.

Standley PC, Calderón S. 1925. Lista Preliminar de las Plantas de El Salvador. La Unió-Dutriz Hermanos. San Salvador.

Steggerda M. 1943. Some ethnological data concerning one hundred Yucatan plants. Smithsonian Institution Bureau of American Ethnology Bulletin 136, Anthropological Papers. No. 29: 189-226.

Steyermark JA, Huber O. 1978. Flora del Avila. Caracas.

Stuessy TF. 2009. Plant Taxonomy. The systematic evaluation of comparative data. 2n Ed. Columbia University Press.

Stuessy TF, Crawford DJ, Soltis DE, Soltis PS. 2014. Plant Systematics. The origin, interpretation, and ordering of plant biodiversity. Regnum Vegetabile. 156: 1-425. Koeltz Scientific Books.

Sutherland CHN. 2008. Catálogo de las plantas vasculares de Honduras. Espermatofitas: 578-580. SERNA, Guaymuras, Honduras.

Swallen JR. 1934. The Grasses of the Yucatán Peninsula. Pubblications of the Carnegie Institution of Washington. 436: 348-349.

Swallen JR. 1936. *Lasiacis* (Griseb.) Hitchc. The grasses of British Honduras and the Petén, Guatemala. Carnegie Institution of Washington Publication. 461: 177-179.

Swallen JR. 1943. *Lasiacis* (Griseb.) Hitchc. In: Woodson RE & Schery RW and coll. (Eds.), Flora of Panama, Part II(1). Annals of the Missouri Botanical Garden. 30(2): 133-139.

Swallen JR. 1953. New grasses from Guatemala. Phytologia. 4(7): 423-427.

Swallen JR. 1955a. Notes on Central American Grasses. Ceiba. 4: 285-288.

Swallen JR. 1955b. *Lasiacis* (Griseb.) Hitchc. Flora of Guatemala. Part II: Grasses of Guatemala. Fieldiana: Botany. 24(2): 184-191.

Swallen JR. 1957. Gramineae (except *Andropogon* and *Paspalum* by Ernest R. Sohns, and *Axonopus* by Geroge Black). In: Maguire B, Wurdack JJ and coll. (Eds.), The Botany of the Guayana Highland – Part II. Memoirs of the New York Botanical Garden. 9(3): 267.

Sylvester SP. 2017. An illustrated generic key and updated list of the grasses (Poaceae) of Belize. Edinburgh Journal of Botany. 74(1): 33-75. https://doi.org/10.1017/S0960428616000275

Tateoka T. 1962. A Cytological study of some Mexican grasses. Bulletin of the Torrey Botanical Club. 89(2): 77-82.

Teerawatananon A, Jacobs SWL, Hodkinson TR. 2009. Phylogenetics of Panicoideae (Poaceae) based on chloroplast and nuclear DNA sequences. Telopea. 13(1-2): 115-142

Thiers B. 2016. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih/. Accessed 1 January 2024.

TROPICOS.ORG. (continuously updated). Missouri Botanical Garden. https://tropicos.org (Accessed 15 March 2025).

Turland NJ, Wiersema 5H, Barrie FR, Gandhi FT, Gravendyck J, Greuter W,, Hawksworth DL, Herendeen PS, Klopper RR, Knapp S, Kusber W-H, Li D-Z, May TW, Monro AM, Prado J, Price MJ, Smith GF, Zamora Señoret JC. 2025. International Code of Nomenclature for algae, fungi, and plants (Madrid Code) accepted by the Twentieth International Botanical Congress Madrid, Spain, July 2024. Regnum Vegetabile 162. Chicago: University of Chicago Press. https://doi.org/10.7208/chicago/9780226839479.001.0001

Tzvelev NN. 1989. The System of Grasses (Poaceae) and Their Evolution. The Botanical Review. 55(3): 142-203.

van't Klooster CIEA, Lindeman JC, Jansen-Jacobs MJ. Index of vernacular plant names of Suriname. Blumea Supplement 15. National Herbarium Nederland, Leiden.

Urban I. 1921. Symbolae Antillanae 8: 1-860. Fratres Borntraeger, Lipsiae.

Ulloa Ulloa C, Acevedo-Rodriguez P, Beck S, Belgrano MJ, Bernal R, Berry PE, Brako L, Celis M, Davidse G, Forzza RC, Gradstein SR, Hokche O, León B, León-Yánez S, Magill RE, Neill DA, Nee M, Raven PH, Stimmel H, Strong MT, Villaseñor JL, Zarucchi JL, Zuloaga FO, Jørgensen PM. 2025, continuously. Vascular Plants of the Americas (VPA) website. TROPICOS. Missouri Botanical Garden, St. Louis, Missouri USA [consulted May 2025]. http://www.tropicos.org/Project/VPA

Vasey G. 1884. The Agricultural Grasses of the United States. Department of Agriculture, Washington D.C.

Villavicencio X, Rúgolo ZE, Renvoize SA. 2014. Poaceae. In: Jørgensen PM, Nee Harley M, Beck SG. (Eds.), Catálogo de las Plantas Vasculares de Bolivia. Monographs in Systematic Botany from the Missouri Botanical Garden. Vol. 127. St. Louis, Missouri, USA.

Villaseñor JL. 2016. Checklist of the native vascular plants of Mexico. Revista Mexicana de Biodiversidad. 87: 559-902. https://doi.org/10.1016/j.rmb.2016.06.017

Vollstädt MGR, Galetti M, Kaiser-Bunbury CN, Simmons BI, Gonçalves F, Morales-érez AL, Navarro L, Tarazona-Tubens FL, Schubert S, Carlo T, Salazar J, Faife-Cabrera M, Strong A, Madden H, Mitchell A, Dalsgaard B. 2022. Plant-frugivore interactions across the Caribbean islands: Modularity, invader complexes and the importance of generalist species. Diversity and Distribution. 28: 2361-2374. https://doi.org/10.1111/ddi.13636

Washbum JD, Schnable JC, Davidse G, Pires JC. 2015. Phylogeny and photosynthesis of the grass tribe Paniceae. American Journal of Botany. 102(9): 1493-1505.

Webster RD. 1988. Genera of the North American Paniceae (Poaceae: Panicoideae). Systematic Botany. 13(4): 576-609.

Wheelwright NT, Haber WA, Murray KG, Guindon C. 1984. Tropical Fruit-eating Birds and their Food Plants: A Survey ofd a Costa Rican Lower Montane Forest. Biotropica. 16(3): 173-192.

White F. 1971. The taxonomic and ecological basis of chorology. Mitteilungen der Botanischen Staatssammlung München. 10: 91-112.

Wiggins IL. 1980. Flora of Baja California. Stanford University Press, Stanford, California.

Zambrana Paniagua NY, Bussmann RW, Hart RE, Huanca ALM, Soria GO, Vaca MO, Álvarez DO, Morán MS, Chávez S, Moreno BC, Moreno GC, Roca O, Siripi E. 2017. Traditional knowledge hiding in plain sight – twenty-first century ethnobotany of the Chácobo in Beni, Bolivia. Journal of Ethnobiology and Ethnomedicine (2017) 13:57. https://doi.org/10.1186/s13002-017-0179-2

Zuloaga FO, Nicora EG, Rúgolo de Agrasar ZE, Morrone O, Pensiero J, Cialdella AM. 1994. Catálogo de la Familia Poaceae en la República Argentina. Monographs in Systematic Botany from the Missouri Botanical Garden. 47: 1-178.

Zuloaga FO, Morrone O, Davidse G, Filgueiras TS, Peterson PM, Soreng RJ, Judziewicz E. 2003. Catalogue of New World Grasses (Poaceae): III. Subfamilies Panicoideae, Aristidoideae, Arundinoideae, and Danthonioideae. Contributions from the U.S. National Herbarium. 46: 1-662.

Zuloaga FO, Morrone O, Saenz AA. 1987. Estudio exomorfologico e histofoliar de las especies americanas del genero Acroceras (Poaceae: Paniceae). Darwiniana. 28(1-4): 191-217.

Zuloaga FO, Scataglini S. 2023. *Panicum* (Poaceae). Flora Neotropica. 124: 1-293. Springer Nature Switzerland AG 2023. https://doi.org/10.1007/978-3-031-33768-0

Appendix I - Index of scientific names cited in the text

(Accepted and valid names in **bold**)

Lasiacis compacta (Swartz) Hitchc., Proc. Biol. Soc. Wash. 24: 145. 1911 = **Lasiacis ruscifolia** (Kunth in F.H.W. von Humboldt, A.J.Bonpland & C.S.Kunth) Hitchc.

Lasiacis divaricata (L.) Hitchc., var. *austroamericana* Davidse, Ann. Missouri Bot. Gard. 64: 374. 1977 = **Lasiacis austroamericana** (Davidse) Baldini

Lasiacis divaricata sensu Auct. Fl. S. America, non (L.) Hitchc. = **Lasiacis austroamericana** (Davidse) Baldini

Lasiacis glabra Swallen, Ceiba 4: 287. 1955 = **Lasiacis ruscifolia** (Kunth in F.H.W. von Humboldt, A.J.Bonpland & C.S.Kunth) Hitchc.

Lasiacis globosa Hitchc., Contr. U.S. Natl. Herb. 17: 251. 1913 = **Lasiacis ruscifolia** (Kunth in F.H.W. von Humboldt, A.J.Bonpland & C.S.Kunth) Hitchc.

Lasiacis grisebachii (Nash) Hitchc. var. *lindelieana* Davidse, Ann. Missouri Bot. Gard. 64: 375. 1977 = **Lasiacis grisebachii** (Nash) Hitchc.

Lasiacis guaranitica (Speg.) Parodi, Notas Mus. La Plata, Bot. 8: 95. 1911 = **Lasiacis maculata** (Aubl.) Urb.

Lasiacis lancifolia Swallen, Publ. Carnegie Inst. Wash. 436: 349. 1934 = **Lasiacis rugelii** (Griseb.) Hitchc.

Lasiacis leptostachya Hitchc., Contr. U.S. Natl. Herb. 22: 19. 1920. = **Lasiacis divaricata** (L.) Hitchc. var. **leptostachya** (Hitchc.) Davidse, Ann. Missouri Bot. Gard. 64: 375. 1977

Lasiacis liebmanniana (E.Fourn.) Hitchc., Proc. Biol. Soc. Wash. 24: 145. 1911 = **Lasiacis ruscifolia** (Kunth in F.H.W. von Humboldt, A.J.Bonpland & C.S.Kunth) Hitchc.

Lasiacis lucida Swallen, Ann. Missouri Bot. Gard. 30: 231. 1943 = **Lasiacis standleyi** Hitchc.

Lasiacis longiligula Swallen, Ann. Missouri Bot. Gard. 30: 232. 1943 = **Lasiacis standleyi** Hitchc.

Lasiacis maculata (Aubl.) Urb. var. *patentiflora* (Hitchc. & Chase) Baldini = **Lasiacis maculata** (Aubl.) Urb.

Lasiacis maxoni Swallen, Ann. Missouri Bot. Gard. 30: 231. 1943 = **Lasiacis oaxacensis** (Steud.) Hitchc. var. **maxonii** (Swallen) Davidse

Lasiacis papillosa Swallen, Publ. Carnegie Inst. Wash. 436: 349. 1934 = **Lasiacis rugelii** (Griseb.) Hitchc.

Lasiacis patentiflora Hitchc. & Chase, Contr. U.S. Natl. Herb. 18: 338. 1917 = **Lasiacis maculata** (Aubl.) Urb.

Lasiacis rugelii (Griseb.) Hitchc. var. *pohlii* Davidse, Ann. Missouri Bot. Gard. 64: 375. 1977 = **Lasiacis pohlii** (Davidse) Baldini

Lasiacis ruscifolia (Kunth) Hitchc. & Chase, Contr. U.S. Natl. Herb. 18(7): 339. 1917 = **Lasiacis ruscifolia** (Kunth in F.H.W. von Humboldt, A.J.Bonpland & C.S.Kunth) Hitchc.

Lasiacis ruscifolia (Kunth) Hitchc. var. *velutina* (Swallen) Davidse, Ann. Missouri Bot. Gard. 64: 375. 1977 = **Lasiacis velutina** Swallen

Lasiacis sorghoidea (Ham.) Hitchc. & Chase, Contr. U.S. Natl. Herb. 18: 338. 1917 = **Lasiacis maculata** (Aubl.) Urb.

Lasiacis sorghoidea (Ham.) Hitchc. & Chase var. *patentiflora* (Hitchc. & Chase) Davidse = **Lasiacis maculata** (Aubl.) Urb.

Lasiacis swartziana (Hitchc.) Hitchc., Bot. Gaz. (Crawfordsville) 51: 302. 1911 = **Lasiacis maculata** (Aubl.) Urb.

Panicum agglutinans Kunth, Enum. Pl. 1: 120. 1833 = **Lasiacis ligulata** Hitchc. & Chase

Panicum arborescens Sieb. ex Trin., Gram. Pan. 208. 1826 = **Lasiacis maculata** (Aubl.) Urb.

Panicum bambusoides Ham. Prodr. Pl. Ind. Occ. 10. 1825 = **Lasiacis divaricata** (L.) Hitchc. var. **divaricata**

Panicum chauvinii Steud., Syn. Pl. Glum. 1: 68 1854 = **Lasiacis divaricata** (L.) Hitchc. var. **divaricata**

Panicum compactum Swartz, Adnot. Bot. 14. 1829 = **Lasiacis ruscifolia** (Kunth in F.H.W. von Humboldt, A.J.Bonpland & C.S.Kunth) Hitchc.

Panicum divaricatum L., Syst. Nat., ed. 10, 2: 871. 1759 = **Lasiacis divaricata** (L.) Hitchc. var. **divaricata**

Panicum divaricatum J.Presl ex Griseb., Fl. Brit. W. Ind. 551. 1864 = **Lasiacis sloanei** (Griseb.) Hitchc.

Panicum divaricatum L. var. *agglutinans* (Kunth) Hack. ex Sodiro, Anales Univ. Centr. Ecuador 1889: 5. 1889 = **Lasiacis ligulata** Hitchc. & Chase

Panicum divaricatum L. var. *glabrum* Kuntze, Rev. Gen. Pl. 2: 784. 1891 = **Lasiacis divaricata** (L.) Hitchc. var. **divaricata**

Panicum divaricatum L. var. *lanatum* Schlecht. & Cham., Linnaea 6: 33. 1831 = **Lasiacis anomala** Hitchc.

Panicum divaricatum L. var. *lanatum* (Sw.) Kuntze, Rev. Gen. Pl. 2: 784. 1891 = **Lasiacis maculata** (Aubl.) Urb.

Panicum divaricatum L. var. *latifolium* Schlecht. & Cham., Linnaea 6: 33. 1831 = **Lasiacis maculata** (Aubl.) Urb.

Panicum divaricatum L. var. *molle* Schlecht. & Cham., Linnaea 6: 33. 1831 = **Lasiacis nigra** Davidse, Phytologia 29: 152. 1974

Panicum divaricatum L. var. *puberulum* Griseb., Fl. Brit. W. Ind. 551. 1864 = **Lasiacis ligulata** Hitchc. & Chase

Panicum divaricatum L. var. *puberulum* Sodiro, Anales Univ. Centr. Ecuador: 5. 1889 = **Lasiacis ligulata** Hitchc. & Chase

Panicum divaricatum L. var. *stenostachyum* Griseb., Fl. Brit. W. Ind. 551. 1864 = **Lasiacis divaricata** (L.) Hitchc. var. **divaricata**

Panicum fruticosum Salzm. ex Steud., Syn. Pl. Glum. 1: 74. 1854 = **Lasiacis ligulata** Hitchc. & Chase

Panicum fuscum Sieb. ex C.Presl, Abh. Böhm. Ges. Wiss. 3: 550. 1845 = **Lasiacis maculata** (Aubl.) Urb.

Panicum glutinosum Lam., Tabl. Encycl. 1: 174, tab. 43, fig. 3. 1791 = **Lasiacis ligulata** Hitchc. & Chase

Panicum glutinosum J.Presl ex Griseb., Fl. Brit. W. Ind. 552. 1864 = **Lasiacis maculata** (Aubl.) Urb.

Panicum grisebachii Nash, Bull. Torrey Bot. Club 35: 301. 1908 = **Lasiacis grisebachii** (Nash) Hitchc., Bot. Gaz. (Crawfordsville) 54: 302. 1911

Panicum guaraniticum Speg., Anales Soc. Ci. Argent. 16: 107. 1883 = **Lasiacis maculata** (Aubl.) Urb.

Panicum latifolium L. var. *tomentellum* Döll in C.F.P.Mart. & auct. suc. (eds.), Fl. Bras. 2(2): 207. 1877 = **Lasiacis anomala** Hitchc.

Panicum lanatum Sw., Prodr. Veg. Ind. Occ. 24. 1788 = **Lasiacis maculata** (Aubl.) Urb.

Panicum lanatum Sw. var. *sorghoideum* (Ham.) Griseb., Fl. Brit. W. Ind. 551. 1864 = **Lasiacis maculata** (Aubl.) Urb.

Panicum latifolium Ham., Prodr. Pl. Ind. Occ. 10. 1825 = **Lasiacis sloanei** (Griseb.) Hitchc.

Panicum liebmannianum E.Fourn., Mex. Pl. 2: 33. 1886 = **Lasiacis ruscifolia** (Kunth in F.H.W. von Humboldt, A.J.Bonpland & C.S.Kunth) Hitchc.

Panicum liebmannianum E.Fourn., var. *depauperatum* E.Fourn., Mex. Pl. 2: 33. 1886 = **Lasiacis ruscifolia** (Kunth in F.H.W. von Humboldt, A.J.Bonpland & C.S.Kunth) Hitchc.

Panicum maculatum Aubl., Fl. Guiana Fr. 1: 51. 1775 = **Lasiacis maculata** (Aubl.) Urb.

Panicum maculatum Rchb. ex Schlecht. & Cham., Linnaea 6: 33. 1831, non Aubl. = **Lasiacis ligulata** Hitchc. & Chase

Panicum maculatum Aubl. var. *pilosum* E.Fourn., Mex. Pl. 32. 1886 = **Lasiacis maculata** (Aubl.) Urb.

Panicum martinicense Griseb., Fl. Brit. W. Ind. 552. 1864 = **Lasiacis maculata** (Aubl.) Urb.

Panicum megacarpum Steud. in Lechl., Berb. Amer. Austr. 56. 1857 = **Lasiacis ligulata** Hitchc. & Chase

Panicum oaxacense Steud., Syn. Pl. Glum. 1: 73. 1854 = **Lasiacis oaxacensis** (Steud.) Hitchc. var. **oaxacensis**

Panicum orinocense Willd. ex Spreng., Syst. Veg. 1: 316. 1825 = **Lasiacis maculata** (Aubl.) Urb.

Panicum praegnans Steud., Syn. Pl. Glum. 1: 74. 1854 = **Lasiacis maculata** (Aubl.) Urb.

Panicum procerrimum Hack., Oesterr. Bot. Z. 51: 431. 1901 = **Lasiacis procerrima** (Hack.) Hitchc.

Panicum rhizophorum E.Fourn., Mex. Pl. 2: 31. 1886 = **Lasiacis rhizophora** (E.Fourn.) Hitchc.

Panicum rhizophorum E.Fourn. ex Hemsl., Biol. Cent.-Amer. Bot. 3: 495. 1885 = **Lasiacis rhizophora** (E.Fourn.) Hitchc.

Panicum rugelii Griseb., Cat. Pl. Cub. 233. 1866 = **Lasiacis rugelii** (Griseb.) Hitchc.

Panicum ruscifolium Kunth in F.H.W. von Humboldt, A.J.Bonpland & C.S.Kunth, Nov. Gen. Sp. Pl. 1: 101. 1816 = **Lasiacis ruscifolia** (Kunth in F.H.W. von Humboldt, A.J.Bonpland & C.S.Kunth) Hitchc.

Panicum ruscifolium Kunth in F.H.W. von Humboldt, A.J.Bonpland & C.S.Kunth var. *amblyoides* E.Fourn., Mexic. Pl. 2: 34. 1886 = **Lasiacis ruscifolia** (Kunth in F.H.W. von Humboldt, A.J.Bonpland & C.S.Kunth) Hitchc.

Panicum ruscifolium Kunth in F.H.W. von Humboldt, A.J.Bonpland & C.S.Kunth, var. *amblyoides* E.Fourn. subvar. *glabra* E.Fourn., Mex. Pl. 2: 34. 1886 = **Lasiacis ruscifolia** (Kunth in F.H.W. von Humboldt, A.J.Bonpland & C.S.Kunth) Hitchc.

Panicum ruscifolium Kunth in F.H.W. von Humboldt, A.J.Bonpland & C.S.Kunth, var. *amblyoides* E.Fourn. subvar. *pilosa* E.Fourn., Mex. Pl. 2: 34. 1886 = **Lasiacis ruscifolia** (Kunth in F.H.W. von Humboldt, A.J.Bonpland & C.S.Kunth) Hitchc.

Panicum scariosum Trin. ex Steud., Nomencl. Bot., ed. 2, 2: 263. 1841 = **Lasiacis procerrima** (Hack.) Hitchc.

Panicum sorghoideum Ham., Prodr. Pl. Ind. Occ. 10. 1825 = **Lasiacis maculata** (Aubl.) Urb.

Panicum sloanei Griseb., Fl. Brit. W. Ind. 551. 1864 = **Lasiacis sloanei** (Griseb.) Hitchc.

Panicum swartzianum Hitchc., Contr. U.S. Natl. Herb. 12: 140. 1908 = **Lasiacis maculata** (Aubl.) Urb.

Appendix II - Nomina excludenda

Lasiacis excavata (Henrard) Parodi, Notas Mus. La Plata, Bot. 8: 92. 1943 = **Acroceras excavatum** (Henrard) Zuloaga & Morrone, Darwiniana 28(1-4): 195. 1987 [1988].

Bas.: *Panicum excavatum* Henrard, Repert. Spec. Nov. Regni Veg. 23: 179. 1926.

Type: "Paraguay, Guarapí, in silvis, 1881, *Balansa 2947*" (holotype: L! [barcode L0044801]; isotypes: BAA (photo!) [barcode BAA00002330], G! (four sheets) [barcode G00009454, G00036486, G00036487, G00036488], K! [barcode K000309354], MVFA (photo!) [barcode MVFA0000426], P! (two sheets) [barcode P00633933, P00633934], US! Fragment from L [barcode 00148483, 00148484]. See comments in Zuloaga et al. (1987).

Appendix III – List of names typified in this revision (reference taxa in the text in brackets)

Panicum divaricatum L. var. *lanatum* Schlecht. & Cham., Linnaea 6: 33. 1831 - (2).

Panicum divaricatum L. var. *glabrum* Kuntze, Rev. Gen. Pl. 2: 784. 1891 - (4a).

Panicum glutinosum Lam., Tabl. Encycl. 1: 174, tab. 43, fig. 3. 1791, non Sw. (1788) - (7).

Panicum lanatum Sw., Prodr. Veg. Ind. Occ. 24. 1788, non Rottb. (1776) - (9).

Panicum guaraniticum Speg., Anales Soc. Ci. Argent. 16: 107. 1883. - (9).

Panicum ruscifolium Kunth, Nov. Gen. Sp. Pl. 1: 101. 1816. - (16).

Panicum liebmannianum E.Fourn., Mex. Pl. 2: 33. 1886. - (16).

Panicum ruscifolium Kunth var. *amblyoides* E.Fourn., Mexic. Pl. 2: 34. 1886 - (16).

Index to collectors cited in the text

The primary collector is cited, even when other collaborators took part in the collecting trip. The collector's name is followed by the collection number (when available) and the respective taxon in parenthesis according to the list of taxa in the text.

J.R. Abbott *15140* (10) - **W.L. Abbott** *179*, *1542*, *2859* (4a); *121, 2597* (7); *332, 737, 16440* (9)- P. **Acevedo-Rodriguez** *3283* (2); *2288*, *2681*, *3795*, *5218*, *6984*, *10931*, *11429* (4a); *3169* (6); *3844* (7); *2638, 3844, 7155* (9) - **L. Acosta** *188* (16) - **M. Acosta S.** *5216*, *10263*, *10696*, *19613* (9); *17148* (10); *5176, 19481* (11a); *20582* (16); *12433* (17) - **R. Acosta** *1668* (4b); *1652* (10) - **C.D. Adams** *601*, *14103* (2); *11638* (4a); *323, 341, 14168* (7); *6399, 8946* (9); *8632* (11a) - **G. Agostini** *1808* (2); *1808* (9) - **G. Aguilar M.** *34, 1615, 4829, 4917* (4a); *1719* (9); *2799* (13); *7385* (16); *4822* (19) - **M. Aguilar** *19* (4a) - **R. Aguilar** *1438* (4b); *11679* (9) - **C. Aker** *449* (17) - **Bro. Alain** *2415* (5) - **D. Alavarez** *2040* (4a) - **P.W. Alcorn** *786* (15) - **R.C. Alexander** *s.n.* (4a) - **A.Alfaro** *33989* (10); *5475* (19) - **E. Alfaro** *3416* (11a); *5597* (14) - **P. Allain** *PA69* (7) - **H.A. Allard** *14126* (4a); *13333, 17779, 21524* (7); *13452, 14557, 20847* (9) - **P.H. Allen** *142, 176, 4102* (9); *367* (13); *137, 797, 2624* (16); *1641, 2376* (17); *1338* (19) - **F. Almeda** *4021* (17) - **J.L.F. Alonso** *5277, 8558* (9) - **A.H.G. Alston** *5267, 5332, 5623* (9); *8292* (10); *5766* (11a) - **C. Alvarado** *26* (4a) - **A.Alvarez** *626, 2019* (10) - **D. Alvarez** *3882* (10); *2211, 8769* (15); *2184* (18) - **P.A.M. Alvarez** *621* (5) - **V. Alves** *4430* (3) - **A.M. Amorin** *2607, 4220, 5278* (7) - **L. Anananch** *101* (7) - **E. Ancuash** *562* (9) - **W.R. Anderson** *37186* (3); *7537* (7); *6950, 8787, 9491, 9777, 9878, 9923, 36296* (9); *12995, 13221* (10); *12668* (16) - **L.M. Andrews** *610A* (7) - **L. Angulo** *551* (17) - **Bro. F. Ansovin** *349* (4a) - **T. Antonio** *5145* (13); *2568* (14) - **R. Aparicio** *15* (16) - **J. Araque** *977* (16) - **M. Araquistain** *1521* (16) - **D. Araujo** *6201* (7) - **F.S. Araújo** *1378*, *1508* (2) - **G. Araújo** *147* (7) - **A. Arauz** *103* (9) - **W.A. Archer** *2759, 8403* (7); *522* (9); *756* (16) - **L. Aristeguieta** *5135*, *6212* (2); *3712* (7) - **J.D.C. Arouck Ferreira** *125* (9) - **L. Arroyo** *1323* (7) - **Bro. Arséne** *s.n.* (4a); *31, 2976, 5287, 8487* (10) - **R. Arvigo** *737* (4a); *48* (18) - **E. Asplund** *14378* (7); *5494, 5496, 5802, 5810, 7272, 8512, 15118* (9); *8669* (10); *12197, 16365, 16632* (11a); *5208, 5687, 5807* (16); *8514* (19) - **G.F. Asprey** *2222* (9) - **D. Atha** *827* (9); *1245* (13); *1013* (15) - **J.T. Atwood** *4182* (13); *3289* (16) - **Bro. B. Augusto** *1015* (4a) - **D.F. Austin** *6651* (4a); **S. Avendano** *351* (10) - **F. Axelrod** *1374, 1583, 3296, 3457, 5364* (4a) - **G. Aymard** *8824* (2); **P.J.M. Baas** *7887* (17) - **C.F. Baker** *2501, 5324* (4a); *3817* (5); *392* (7); *3790* (15); *2105* (16); *2454* (17); *4587* (18) - **M.A. Baker** *6307* (9) - **B. Balansa** *40a* (3); *40, 41* (9) - **R.M. Baldini** *2118, 2119, 2121* (7) - **J.T. Baldwin Jr.** *14342* (10); *3538* (13) - **M.J. Balick** *2053* (4a); *1491* (7) - **H. Balslev** *10593* (9) - **P. Bamps** *s.n* (9) - **M. Bang** *494* (3); *1289* (9) - **M.R. Barbosa** *2531* (9) - **P.J. Barbour** *5432* (7); *2693* (10) - **G.W. Barclay** *2058* (16) - **F.A. Barkley** *39669* (4a); *1831* (9) - **G. Barrantes** *s.n.* (13) - **S. Barrier** *2997* (4a) - **K. Barringer** *3924* (10) - **B. Bartholomew** *3524* (4a); *2769* (10); *2538* (13); *3* (18) - **H.H. Bartlett** *17404*, *17312*, *17558* (4a); *11505, 12190* (5); *8576* (7); *12954* (9); *10796* (16); *17498, 17519* (18) - **M.S. Bass** *231* (17) - **I. Basualdo** *1399* (7); *1551* (9) - **J. Bauml** *464* (4b); *464, 586B* (9); *453* (10) - **R. Bavazzano** *s.n.* (10); *s.n.* (14) - **G. Beck** *395*, *24751* (3); *6874, 12287, 19303* (7); *1668, 2590, 4727, 6985, 9177, 18633* (9) - **J. Beckner** *2633* (16) - A.**A. Beetle** *2216, 4617, 5925* (10); *5790* (13); *957* (16) - **C. Belanger** *70* (4a); *71* (9) - **R.P. Belém** *1657* (7) - **C.M. Belshaw** *3086, 3615* (7); *3086* (9); *3615* (17) - **B. Bennett** *3527* (17) - **W. Berendsohn** *1377* (4a) - **S. Bergeron** *315* (7) - **L.A. Bermúdez** *34933* (20) - **T. Bermúdez** *66* (19) - **L.C. Bernacci** *162* (3) - **R. Bernal** *1127* (13) - **L. Bernardi** *20372, 20561* (9); *993* (13) - **G. Bernoulli** *48* (4b); *1189* (11a); *1189* (13) - **C. Bertero** *s.n.* (7); *s.n.* (9) - **B.S. Bertoni** *2672* (9); *3231* (16) - **J. Betancur** *4975* (9); *767* (10); *1341* (13) - **Biolley** *3114* (12) - **G.A. Black** *46-185, 52-14444, 54-16333*, *54-16532* (7); *48-2495* (13) - **S. Blackmore** *2014* (11a); *4000* (16); *2145* (17) - **S.F. Blake** *7721* (10); *7836* (13) - **K.E. Blum** *1962* (9); *2089* (11a); *1734* (13); *7268* (19) - **J.D. Boecke** *2095, 2862* (10) - **I. Boldingh** *990, 2645* (4a); *750* (6) - **G. Bolland** *38* (7) - **J. Bono** *768* (4b); *8* (7); *184, 2694, 4075, 4987, 6954, 8111* (9); *7230* (10) - **B. Boom** *6070* (2); *6975* (4a); *7332* (7); *6418* (13) - **W. Boone** *1357* (7) - **B. Bordenave** *901* (7) - **M. Botteri** *149* (10); *150, 151* (14) - **E. Bourgeau** *1299, 1936, 2648* (10); *1461, 2648* (11a); *2971* (13) - **Boutin** *5132* (4b) - **M.G. Bovini** *104* (7) - **H.E. Box** *64, 91, 172* (4a); *115, 160* (9); *119* (18) - **B. Boyle** *1798* (10) - **L.J.K. Brace** *1617, 4230* (4a) - **J. Bradford** *#327* (4a) - **K. Bradley** *#1141* (4a) - **P.I.S. Braga** *2465* (9) - **J. Brandbyge** *32136* (7) - **D.E. Breedlove** *29030, 47298, 55240, 55368* (4a); *13704*, *28304* (4b); *28838, 38201* (5); *6428, 13121, 13208, 13956*, *14829, 20352, 27616, 28156* (10); *13903, 54023, 54688* (11a); *24080* (13); *14999* (14); *13247, 28329* (16); *33955, 34090* (17); *55237* (18) ; *13566* (19) - **A.M. Brendes** *21911* (5); *20319* (19) - **A.M. Brenes** *1733, 21959* (9); *5191, 20314* (10); *17380* (11a); *20300, 21101, 21703, 27923* (14) - **F.J. Breteler** *3417* (9); *4136* (10); *3* (11a); *4128* (13) - **S.W. Brewer** *172* (5); *171* (11a) - **H.S. Brito** *03* (7) - **E.G. Britton** *187, 6403* (4a); *1230* (7) - **N.L. Britton** *2905* (2); *241*, *946*, *2130*, *2630*, *4955*, *5696*, *15134* (4a); *678, 2266, 4490* (7); *443, 665, 2623, 4045, 4694, 6450* (9); *106, 14860* (15); *1509, 1624, 12979, 14659, 15065* (16); *393, 759, 1280, 15134* (18) - **G.K. Briziky** *253* (4a) - **W.E. Broadway** *2504*, *2627*, *6736*, *6775*, *8081*, *8083* (2); *415, 3551, 4038, 4052, 5504, 5892, 6811, 7666, 9929* (7); *164, 501, 607, 671, 716, 4294, 4674, 4841, 4976, 5170, 5991, 6397, 7067, 7233, 9064* (9); *289* (18) - **N.V.L. Brokaw** *60* (5) - **B.M. Broom** *6911* (7) - **W.C. Brumbach** *8732* (4a) - **J. Brunken** *348, 440* (10); *316* (16) - **D.R. Brunner** *1200, 1775, 1850* (9) - **M. Brunt** *2031*, *2191* (4a) - **O. Buchtien** *2499* (7); *89, 161, 3635* (9) - **G.S. Bunting** *6645* (2); *1167, 6002, 6046, 12242* (9); *4901* (10); *527, 8990* (11a); *5685, 10016* (16) - **C. Burand Jr.** *281* (2); *298* (16) - **D. Burch** *1187* (16) - **W.J. Burchell** *703* (7) - **W.C. Burger** *8402* (10); *9629* (14); *4117, 7855* (16); *4482* (19); *7855* (20) - **A. Burkart** *28253* (3); *18338* (9); *17001* (10) - **L. Buscalioni** *4079* (2); *1252*, 2871, *2959*, *4570* (7) - **P. Busey** *574* (16) - **Bustamante** *35* (13) - **W.M. Buswell** *11* (4a) - **R. Byrne** *227* (4a) - **E. Cabrera** *57, 146, 589, 700, 3607*, *8784*, *9056*, *9290*, *9581*, *9781*, *12984*, *14477* (4a); *440* (5); *99, 1129* (15); *2032* (16); *393, 7232* (18) - **S. Cafferty** *33* (13) - **G. Calatayud** *4342* (7) - **C. Calderón** *2327, 2522* (7); *83* (14); *2091* (17) - **G.M. Calderón** *120, 1561* (16) - **J.G. Calderón V.** *217* (11a) - **S. Calderón** *508* (4b); *509, 2514* (9); *507, 1324* (11a); *849* (13); *510* (16) - **R. Callaway** *10898* (16) - **J. Callejas** *4728* (13) - **R. Callejas** *4050, 9014* (9); *3311, 7913, 11331* (10); *9014* (16); *9190* (19) - **Calónico** *21308* (11b); *21134* (18) - **J.I. Calzada** *24618* (10); *3964* (13); *534* (16) - **W.H. Camp** *911, 2461, E-3039* (9); *2461* (10) - **D.G. Campbell** *22147* (7) - **A. Campos V.** *2503* (14) - **J. Campos** *2714*, *4062* (3); *2233, 4105* (9) - **J. Caranqui** *177* (9) - **R.A. Carballo** *484* (4b); *444* (8); *1042* (13); *1142* (14); *888* (16); *444* (19) - **G. Carnevali** *5656* (4a) - **A. Carter** *3110* (9); *2023, 3110* (16) - **H. Carter** *7007* (7) - **R. Carter** *5325* (4a); *5321* (9) - **A.M. de Carvalho** *6973* (3); *1314, 3196, 3532* (7); *6973* (9) - **A. Cascante** *1436* (13) - **E.D. Castellani** *150* (3) - **R. Castello** *47* (10) - **A. Castillo** *584* (2); *1878*

(16) - **J.F. Castrejon R.** *925* (4b) - **D. Castro** *2420* (9) - **E. Castro** *100* (9); *168* (11a); *252* (19) - **S. Castroviejo** *405* (9); *s.n.* (10) - **C. Catalan** *114* (10) - **J.C. Catari** *58* (7) - **L. Catasús Guerra** *s.n.* (5) - **P.C.D. Cazalet** *5125* (17) - **L. Cayola** *1678* (7) - **J.A. Cedeño** *438* (4a); *238* (7); *637* (9) - **R. Cedillo** *2351* (10) - **C. Centeno** *248* (19) - **C.E. Cerón** *1355* (7); *2118*, *4609, 18279* (9); *20374* (11a) - **M.F. Cervantes** *825* (4a) - **R. Chacón** *146, 213* (10); *75, 383* (16) - **K.L. Chambers** *2608* (9) - **C. Chan** *6049* (15) - **M.L. Chaparro** *107* (13) - **C.E. Chardon** *811* (4a) - **A. Charpin** (9) - **A. Chase** *8619*, *9437, 9644* (3); *3930, 6157, 6192, 6431, 6521, 6587, 6683, 6726, 6782, 6814* (4a); *6228*, *6742* (6); *6454*, *6747, 7833*, *8027, 8610, 9103, 9794, 9796, 10969*, *11321* (7); *6218, 6412, 6419, 6457, 6728, 6824, 10152, 11019, 11154, 11618, 11821, 12339, 12580* (9); *12408* (10); *12464* (13) - **U. Chavarria** *1627* (4a); *1627* (4b); *208, 287* (16); *1943* (17) - **J.L. Chaves** *1409* (9); *15* (16) - **A.M. Chickering** *9* (16) - **Chinchilla Peña** *ISB00584* (13) - **M. Chorley** *341* (4a) ; *342* (14); *407* (16); *342* (19); *170* (20) - **H.W. Churchill** *4342* (19) - **C.A. Cid** *4624* (7) - **J. Cisneros** *20* (16) - **J.L. Clark** *9117* (9); *3557, 9339* (17) - **D. Clarke** *6666, 7997, 8637* (7); *5145, 8219* (9); *30* (13) - **P. Claussen** *192* (7) - **W.D. Clayton** *4977* (9) - **Clement** *596* (4a); *270* (9) - **Bro. Clemente** *2879* (4a); *5683* (16) - **A.Cóbar** *998* (16) - **T.S. Cochrane** *6296* (19) - **A. Cogollo** *1413* (7) - **R. Combs** *55* (18) - **J. Conrad** *3064* (10); *2966* (16); *2986, 3253* (18) - **E. Contreras** *2448, 8838* (4a) ; *1596* (5); *2283* (9); *5972* (10); *1151, 1738, 2692* (15); *3327, 4270, 7425, 9437, 10492* (17); *72, 1395, 1518, 1689, 1846, 3641* (18) - **C. Conzatti** *2012* (10); *1103* (16) - **O.F. Cook** *923* (3); *1405* (9) - **G.R. Cooley** *8182* (9) - **J.J. Cooper** *98* (10) - **Coradin** *7787* (9) - **E.L. Core** *805* (9); *477* (10) - **L. Cormier** *88* (7) - **I. Coronado** *454* (11a); *4974* (12); *5488* (13); *2568, 3555, 3566, 5053, 5446* (16); *1584* (17) - **M. Correa** *6* (4a); *885* (9); *2869* (10); *7365* (12); *2262* (13); *3351* (17) - **D.S. Correll** *5974, 40304, 40321, 40919, 43636*, *43383*, *43906*, *45128*, *45609*, *46073*, *46438*, *47652*, *53983*, *54043* (4a) - M.E. Cortes *472* (4a) - **Costa** *641* (7) - **C. Cowan** *3223* (4a); *2796* (9); *3374, 5033* (10); *5047* (13); *5029* (16); *3153* (18) - **R.S. Cowan** *1486, 38105, 39007* (7); *1448, 1484, 1572* (9); *1889* (13) - **H.C. Cowles** *012-2* (4a) - **G. Cremers** *7761, 13869, 14008, 14455, 14636* (7); *14455* (9) - **T.B. Croat** *54399* (2); *23707, 23924, 24420, 40006, 40038, 41779, 42537*, *63055*, *68495* (4a); *23398* (5); *19761*, 20302, 21008, *53744*, *56617*, *62602, 81977* (7); *26858* (8); *4259, 4821, 8009, 12791, 12924, 12942, 18083, 21968, 22050, 22513, 23187, 26615, 36013, 48019, 55821, 64486, 84613, 88484, 91906, 99051* (9); *14603, 39510, 42290, 63325, 63424, 69119, 71510, 87675*, *89584, 94556, 95117* (10); *7081, 21700, 69848* (11a); *12142, 14221, 17287, 25353, 37418, 63734* (12); *6108, 12037, 33410, 40779, 68210* (13); *63145, 41390* (14); *24709, 24770, 41538* (15); *9642, 9739, 24618, 41532, 63308, 63555, 64094* (16); *74, 13950, 22169, 44409, 63308* (17); *23912, 65305* (18); *4482, 22331, 22784, 33047, 39093, 66260A, 70702* (19) - **L. Croizat** *677* (7); *250* (17) - **M.R. Crosby** *1099* (4a) - **Cruz** *27* (3) - **H. Cuadros V.** *440* (9) - **J. Cuatrecasas** *4191* (2); *22174* (3); *2995, 15202* (7); *2008, 2996, 9624, 12239, 13884, 15069, 19617, 25693* (9); *221, 14980, 15358, 22174, 25306, 28941* (10); *25383* (14); *22909, 24922* (16); *13674* (17); *15602* (19) - **N. Cuello** *685* (13) - **G. Cufodontis** *180* (9) - **H.M. Curran** *s.n.* (2); *223* (9) - **A.H. Curtis** *3588, 5530* (4a); *291, 520* (16) - **W.N. da Fonseca** *323* (7) - **D.C. Daly** *D348, D478, 6386, 6856* (7) - **B.E. Dahlgren** *198* (17) - **W.G. D'Arcy** *13493* (9); *6748, 14961* (12); *12254* (13); *9619* (16); *10838, 14348, 14705* (17); *14521, 18050* (19) - **Da Rocja** *109* (3) - **Dasa** *4911* (13) - **R. Daurenmire** *438* (9); *399* (13); *169* (16) - **G. Davidse** *2758, 2875, 2580,, 2892, 3047, 3087, 3103, 3104, 3184, 3241, 4772A, 5692, 21062* (1); *2522, 2591, 2696, 2786, 3690, 3968, 4272, 4469, 4617, 15229*, *26374* (2); *2189, 3114*, *10948* (3); *2126, 2174, 2196, 2226, 2295, 2440, 2619, 2641, 2674, 2721, 3258, 3274, 20120, 20211, 20461, 20623, 29441* (4a); *2145, 37114* (4b); *2218, 2442, 36262* (5); *3242, 3248* (6); *2461*, *2566*, *2579*, *11500*, *13648*, *12241*, *19775* (7); *2100, 2121, 2839, 10162, 10816A*, *24055, 34756, 37167* (8); *452, 2197, 2446, 2460, 2561, 2680, 3247, 3250, 3266, 3923, 4782, 4968, 5163, 5198, 5469, 5522, 5585A, 5605, 5629, 5690, 5692, 5727, 9409, 12544, 19795, 21470, 21834* (9); *2025*, *2035*, *2098*, *2119*, *2126*, *2209*, *3033*, *3100, 3240, 3999, 4032, 9458, 9819, 10155, 21206, 22347, 23370, 24620, 24655* (10); *2026, 2127, 2199, 2205, 2346, 3113, 4980* (11a); *2199* (11b); *10103*, *20402* (12); *2072, 2081, 2161, 2347, 2910, 3022, 3193, 4783, 5523, 5764, 20890* (13); *10158, 12489, 21089, 23385, 29728, 37158* (14); *20094*, *20142, 20261, 31968* (15); *2033, 2082, 2169, 2190, 2379, 3012, 3120, 3125*, *4220, 5020, 20213, 34518* (16); *2173, 20420, 23384, 26272, 32159, 36944* (17); *2200, 2388, 3116, 3249, 3264, 3273, 4969, 9732* (18); *20448, 23354, 36712* (19); *2162, 2188, 12508* (20) - **C. Davidson** *10580* (7) - **M.E. Davidson** *710* (10) - **N. Dávila** *784* (4b); *4988* (9) - **E.Y. Dawson** *26547* (4a) - **O. de Benavides** *9707* (10) - **L. de Escobar** *2690* (10) - **R. de Filipps** *191* (9) - **J.J. de Granville** *13048* (2); *1380, 6982, 9320, 13048, 14294, 15207, 15880, 16318, 1648, 17393* (7); *13812, 15207, 15518, 15880, 16318* (9) - **J. de Jesus Jiménez** *2764*, *5937* (4a); *2123, 3468* (9) ; *3751* (18) - **J.S. de La Cruz** *3663, 4291* (7) - **R. de Lemos Fróes** *21119* (13) - **G. de Nevers** *4927* (9); *4350* (13); *4441* (17) - **M. de Pardo** *139* (7) - **L.P. de Queiroz** *1008* (3); *1383, 2473, 6379* (7); *10383* (9) - **R.R. de Santos** *1264* (7) - **O. Degener** *26713* (5); *26291* (10); *26290* (13); *26760* (16) - **N.B. Degignani** *1302* (3); **A. Delgado** *950* (17) - **C. Delnatte** *3674* (9) - **Del Puerto** *2663* (3); *2648* (16) - **M. Dematteis** *559, 2228* (9) - **W. Devia A.** *579* (13) - **C. Diaz** *7905* (7); *3508* (9) - **W. Diaz** *1253* (2); *3134* (9); *532* (13) - **M. Díaz-Piferrer** *s.n* (4a) - **J. Dickson** *271* (16) - **A. Dik** *1388* (17) - **M.O. Dillon** *4360* (10) - **R.H.L. Disney** *A380/D* (4a); *A380/D* (16); *A380/D* (18) - **C.W. Dodge** *16513* (4b); **C.H. Dodson** *7666* (7); *11398* (9); *10230, 12245* (10); *11309A* (16) - **Donaire** *22* (4b) - **J. Donnell Smith** *4891* (9); *1852* (10) - **J. Dorantes** *2261* (13) - **L.J. Dorr** *6298* (9) - **E.B. dos Santos** *69* (7) - **T.S. dos Santos** *51* (7) - **R.L. Dressler** *5* (16) - **H. Droege** *428* (4a) - **E. Dryander** *1895* (10); *2555* (11a) - **A.P. Duarte** *5221* (7) - **F. Duckett** *212* (4a); **D.A. Dudey** *778, 1948* (16) - **T.R. Dudley** *10025* (17) - **J.A. Duke** *15495* (4b); *7607* (9); *13704(4)* (10); *5107A* (11a); *5959* (13); *5702* (16); *10098(3)*, *15311* (17) - **K. Dumont** *7405* (2) - **R. Duno de Stefano** *2170* (4a) - **P. Dusén** *9643* (3); *11487, 14050* (7) - **P. Duss** *769, 770, 3182, 3613* (9) - **J.D. Dwyer** *9957*, *10971, 11155, 12209, 11239, 14522, 14899, 15136* (4a); *544* (5); *9753* (7); *4011, 7150, 11994* (9); *1967* (11a); *11942 A* (11b); *7974* (12); *1820, 7800, 8724, 11416* (13) ; *12284* (15); *1752, 2529, 2598, 4181, 11005, 11274* (16); *2977, 4549* (17) - **A.A. Eaton** *315* (4a) - **J.E. Ebinger** *1067* (9); *858* (16); *340* (17) - **D.K. Edelman** *02* (4a) - **M.T. Edwards** *478* (16) - **P.J. Edwards** *207* (3) - **H.F.A. Eggers** *13480* (2); *10* (4a); *15006* (9) - **W.A. Egler** *47665* (7) - **G. Eiten** *4092*, *10750* (2); *4736* (3); *4320, 5955A, 6279* (7) - **E.L. Ekmann** *618* (3); *1020*, *1723, 2334, 5845, 8559, 11246, 11527, 14971* (4a); *1024*, *10506*, *12646*, *13046*, *13462*, *13511*, *13531*, *16464*, *17542*, *18340* (5); *14176* (6); *619, 2224, 2624, 4330, 10095, 10108, 10318, 10324, 11157, 13200, 13878, 14219* (9); *2841, 7153, H7153* (11a); *4254, 10306, 11526, 12446, 12845, 13516, 14531, 15242, 16157, 16489* (15); *4903, 6535, 7578, 7699, 11721, 15318* (16); *653, 2190, 10557, 11528, 12094, 12743, 12853, 13035, 15319, 15851* (18) - **Bro. Elias** *1098* (16) - **T.S. Elias** *1667A* (9) - **M. Elizondo** *20* (14) - **H. Ellenberg** *290* (13) - **L. Emygdio** *1217* (7) - **F. Encarnación** *26216* (7) - **C.O. Erlanson** *308* (11a); *383* (13) - **W.R. Ernst** *1156* (4a); *1113* (9); *2285* (16) - **L.E. Escobar** *ISB00748* (11a) - **C. Espadas** *106* (16) - **J. Espina** *2010* (9) - **F. Espinal** *112* (10) - **J.A. Espinosa Jimenez** *534* (8) - **F. Espinoza A.** *3451* (19) - **R. Espinoza** *528* (4a); *1726, 1780* (9) - **M. Esteban** *22885* (10) - **A.**

Estrada *1502* (4b); *1843* (10); *1783* (13); *1488* (17); *2029, 2684* (19) - **J. Eugenio** *284* (2) - **R. Evans** *1163B* (8); *1163A* (13); *1315* (17) - **W.J. Eyerdam** *326* (4a); *594, 12079* (9) - **F. Fagerlind** *1961* (9); *1594* (17) - **N.C. Fassett** *29100* (10); *28590* (11a) - **C. Feddema** *131* (10); *2544* (16) - **A. Fendler** *963* (2); *1613*, *1614*, *1615*, *1617*, *2493* (3); *371, 2494* (9); *1619* (10); *2495* (13) - **B. Ferlay** *1620* (4a); *1172* (9) - **Á. Fernández** *12764*, *26980* (2); *84* (4a); *7567* (7); *1188* (10) - **A. Fernandez-Pérez** *5194* (16) - **J. Fernandez Casas** *6039* (9) - **A. Ferreira** *125* (7) - **R. Ferreira** *920, 7916* (7) - **R.S. Ferris** *5848* (13); *5656* (16) - **M.S. Ferrucci** *1053* (7) - **T. Feuerer** *855a* (9) - **P. Fiaschi** *1392* (3); *1512, 1629* (7) - **K. Fiebrig** *4710, 6014* (9) - **H. Field** *s.n.* (4a) - **C.S. Figueredo** *788* (7) - **V.M. Figueroa** *156* (4a); *164* (12) - **T. Filgueiras** *2445* (7) - **G.L. Fisher** *35298* (10); *46193* (16); *37127, 37129* (18) - **W.C. Fishlock** *140*, *240* (4a); *140* (9) - **E. Fittkau** *118* (7) - **M. Fleury** *1581* (7) - **G. Flores-Franco** *3673, 4007* (13) - **N. Flores** *71* (16) - **J. Florschütz** *1563* (2); *1563* (9) - **J.P. Folsom** *7044* (9); *6932* (12) ; *6431* (13); *4845* (19) - **R. Fonnegra** *7731* (9); *2400, 6603* (10); *6954* (13); *1459, 6996* (16) - **E. Forero** *6310* (7); *5173* (9); *2231* (10) - **R. Fortunato** *3778* (3) - **F.R. Fosberg** *58915* (4a); *27757, 55312* (7); *19519*, *19777, 21990, 59223* (9); *19635, 20532, 23149* (10); *20370* (19) - **P.F. Foster** *571, 595* (7) - **R.B. Foster** *3487, 6832* (7); *2026* (13) - **Fournet** *4272, 4482* (9) - **D. Frame** *139* (7) - **F. Franco** *2975* (16) - **L. Franco Mellado** *2559* (10) - **P. Franco** *1056* (11a) - **A. Fredgolm** *5532* (4a) - **W.G. Freeman** *11426* (7) - **E. Freid** *04-109, 06-048, 06-761* (4a) - **A. Freire-Fierro** *3613* (11a) - **G.F. Freytag** *319* (10) - **Friedrichstahl** *549* (9) - **P. Fryxell** *2842* (4a); *3281* (4b); *3696* (16) - **A. Fuentes** *6962* (3); *7041* (9) - **Bro. M. Fuertes** *130*, *1276* (4a) - **N. Funck** *813* (11a) - **D.G. Furth** *10* (16) - **C. Galdames** *3459* (8); *1811* (13); *484* (19) - **H. Galeotti** *5725* (10); *5717* (13) - **W. Galiano** *4864, 6620* (9) - **Galo** *77* (4b) - **N. Galué** *120* (16) - **B. Gamboa R.** *2064* (10) - **M. Gandoger** *s.n.* (18) - **W. Ganev** *1768*, *2846* (3) - **G. Gann** *529* (4a) - B.**H. Garcia** *6458* (9) - **J. Garcia R.** *388* (10); *929* (11a) - **M. Garcia** *1818, 2401* (10); *2220* (16) - **R. Garcia** *569* (4a); *840* (15) - **G. Gardner** *1894*, *3513* (2); *5654* (3); *3573*, *4052* (9) - **Bro. A. Garnier** *39* (11a) - **N. Garwood** *81, 2282A, 1741A* (9); *185* (17) - **E.M. Gaudichaud** *303 bis* (7); *303* (9) - **G.F. Gaumer** *129, 1032* (4a); *1032, 23685* (15); *878* (16) - **R. Gegen** *1155* (3) - **W. Gehringer** *398* (4b) - **P.H. Gentle** *3657*, *4905*, *5572*, *6278*, *6931*, *6963*, *7785*, *7975*, *8215*, *8523* (4a); *4798*, *6849*, *7101*, *7523*, *8384*, *8441*, *8864*, *9641* (5); *1910, 2196, 6945, 7873, 8118* (9); *1769, 3937, 7205, 7874, 9331* (11a); *1743, 3632* (13); *1218, 8094, 8974, 9691* (15); *104* (16); *4398, 6366, 9023* (17); *6966, 8980* (18); *7205* (19) - **A. Gentry** *51046* (4a); *29418, 37939, 48146* (7); *9992*, *13488, 16430, 28320, 29489, 34876*, *61089, 70169, 70736* (9); *28731* (10); *5126, 17724* (13); *2290, 2402, 8319, 58299* (16); *3511, 3514, 3515, 6897* (17); *13855, 14090, 28662* (19) - **H.S. Gentry** *4981, 7097* (16) - **Gerdes** *s.n.* (3) - **R.E. Gereau** *1981* (4a); *2235* (16) - **D.R. Gifford** *G71* (9) - **L.J. Gillespie** *866* (13) - **W.T. Gillis** *7338, 7769, 5696* (4a) - **D.A. Giraldo Cañas** *708* (9) - **C. Girod** *3159* (7) - **A.M. Giulietti** *2064, 13724* (7) - **S.F. Glassman** *1972, 1625* (8); *1947* (10); *1732* (20) - **A. Glaziou** *18649, 20574* (3); *1007* (7) - **H.A. Gleason** *70* (7) - **R.K. Godfrey** *66850* (9); *66916* (19) - **A. Goeldi** *38, 227* (7) - **D. Goldman** *1994* (4a) - **A. Goméz** *99* (10) - **L.G. Gomez** *24501* (11b) - **P. Goméz** *499* (9) - **J. Gómez Laurito** *1068, 1082* (9); *2655* (10); *262, 1703, 3049, 12813* (13); *136, 258* (16) - **R. Gonto** *5902, 6633* (10) - **A. Gonzales** *469* (9) - **F. González** *FG 2813* (7); *753* (19) - **J. González** *334* (10); *1688* (11a); *2576* (13) - **M. Gonzalez-Espinosa** *166, 865* (10) - **R. Goodland** *955* (2); *715* (9) - **I.S. Gottsberger** *22* (9) - **F.W. Gould** *15047* (4a); *10892* (9); *12250* (13) - **E. Gounelle** *s.n.* (3) - **J. Graham** *516, 16158* (7) - **J.R. Grant** *3283* (9); *92-01974* (16); *2216* (17); *1824* (19) - **M.L. Grant** *10549* (7) - **V. Grant** *821* (14) - **M. Grayum** *11530* (4a); *6078* (4b); *4737* (9); *8450* (10); *4736* (11a); *8430* (14); *4157* (16); *10813* (18); *6118, 6208, 8430* (19) - **J.M. Greenman** *5289* (11b) - **A. Grijalva** *3597* (4a); *4185* (4b); *2094* (11a); *623* (14); *1870* (16) - **A. Gröger** *561* (2) - **M. Groppo** *481* (7) - **P.J. Grubb** *1521* (17) - **E.R. Guaglianone** *2817* (3); *675* (9) - **G.F. Guala** II & al. *1901* (4a) - **F. Guanchez** *2101* (13) - **E. Gudiño** *531* (17) - **M.L. Guedes** *6654* (7) - **C. Guerra** *595* (9) - **B. Guerrero** *275* (10) - **G. Guevara** *41* (4a) - **M. Guillemin** *739* (3); *826* (7) - **R. Guillën** *1418, 3675, 4585* (7) - **C. Gutierrez B.** *1614* (15) - **G. Gutiérrez** *128* (9); *170145* (13) - **N. Gutiérrez** *538* (10) - **M. Guzmán** *1614* (11b) - **R. Guzmán** *765* (11a) - **W.A. Haber** *718, C.2266, 4/2001* (10); *9616* (11b); *11702* (12); *9716* (14); *9609* (19) - **J.L. Hage** *1134, 2109* (7) - **L. Hahn** *480* (4b); *1158* (7); *482, 1057* (9) - **W. Hahn** *3663, 4349, 5634* (7); *699, 2250, 2302* (9); *4520, 5715* (13); *253* (19) - **R.B. Hamblett** *1874* (16) - **C. Hamilton** *2835, 2956* (9); *1037* (13); *1244* (14); *2736* (17) - **M.A. Hamilton** *480* (4a); *1189* (12) - **B. Hammel** *6941* (8); *3275* (9); *1209, 1765, 4701, 5370, 15696, 23541* (10); *8479* (11a); *5125* (12); *5275* (16); *1672, 8404, 17386* (17); *1310, 18054* (19) - **R.J. Hampshire** *59* (8); *1267A* (13); *1295* (16); *59, 700* (19) - **O. Handro** *910* (3) - **J. Harlow** *73* (16) - **E.P. Heringer** *15220* (7) - **R.M. Harley** *16991* (2); *21784, 28543* (7); *11074, 21784* (9) - **G. Harling** *256* (9) - **W.E. Harmon** *647* (5); *4278* (10); *4280* (14) - **N.A. Harriman** *17501* (7) - **W. Harris** *11297*, *11490*, *11528*, *11530*, *12512, 12629*, *12691*, *12740, 12572, 12768* (4a); *11354, 11486*, *11487, 11552, 11587* (6); *11398*, *11405*, *11410*, *11469*, *11491*, *12488*, *12650*, *12768* (9); *11832, 12615, 12828* (11a); *11469, 11491* (16); *11260, 11454, 11490, 11531, 11589* (18) - **D. Hartlett** *649* (10) - **C.V. Hartmann** *13* (7); *50* (16) - **R.L. Hartmann** *12275* (17) - **L.H. Harvey** *8598* (5) - **E. Hassler** *8920* (3); *2868, 3731, 9143, 12514* (9) - **W.H. Hatheway** *1689* (10) - **G. Hatschbach** *31338*, *58458*, *71073* (3); *974, 14091, 46792*, *57047* (7); *15844*, *16608*, *39881, 57047, 74460* (9) - **O.L. Haught** *3633* (16); *2973* (17) - **J.G. Hawkes** *1921* (9); *2131* (11a); *2192* (14) - **T. Hawkins** *1334* (9); *1531A* (10); *1669* (15); *1644* (18) - **A.A. Heller** *4375* (9) - **T.W. Henkel** *967, 4940* (7); *2831, 5590* (9) - **J. Henriquez** *14* (16) - **S. Henriquez** *5174* (9) - **N. Hensold** *1035* (10) - **D.N. Hepper** *13, 54* (10) - **Bro. Heriberto** *257* (9) - **A.I. Hernández** *119* (11a) - **E. Hernandez X.** *309* (14) - **H.M. Hernández** *479* (10) - **A. Herndon** *1765* (4a) - **G. Herrera** *2010* (4b); *4735* (9); *3601* (14) - **H.A. Hespenheide** *1409* (4a) - **N.M. Heyde** *10* (7); *3906* (13); *3915* (14); *3899* (16) - **S.R. Hill** *2289, 3294, 10988, 25372, 28897* (4a); *13012* (7); *28989* (9); *1681* (14) - **G.B. Hinton** *1909, 4958, 6722, 9581, 14932, 15156* (10); *1948, 2408* (13); *10809, 10809a, 11381, 14633* (14); *1767, 4847, 15156* (16) - **A.S. Hitchcock** *5946*, *2564*, *10001*, *10021*, *10136*, *10177*, (2); *22616* (3); *409*, *410*, *411*, *723*, *7311, 9149, 9264, 9304*, *9519*, *9687*, *9802*, *9838*, *9881*, *16354*, *19888* (4a); *8722* (4b); *588, 9730, 16468* (6); *9962, 10020, 10151, 10170, 10261, 10262, 10269, 10275, 17553*, *21863, 33391* (7); *8201* (8); *416, 417, 592, 593, 594, 8674, 8695, 8921, 9036, 9053, 9335, 9380, 9382, 9569, 9570, 9571, 9808, 9813, 9893, 10064, 10170, 10270, 10374, 10731, 16353, 16415, 16454, 20133, 20236, 20295, 20432, 20607, 21196, 21808, 22118, 22652, 23325* (9); *409, 415, 6680bis, 7207, 8269, 8270, 8286, 8311, 8315, 8925, 9057, 20754, 21184, 21856* (10); *412, 8199, 8201, 8488, 8496, 8672, 8698, 8853, 8877, 9045, 9080, 9107, 9608, 9800, 20299, 20568, 21131* (11a); *8281, 8695* (11b); *6385, 6422, 8572, 8694, 7961, 8393, 9067* (13); *413*, *8502, 9051* (14); *176* (15); *411, 414, 8060, 8068, 8570, 8571, 8577, 8581, 8676, 8710, 8743, 8763, 8850, 8979, 8982, 9204, 20037, 20057* (16); *20438* (17); *410, 590, 591,8673, 9413, 9606, 9801* (18); *8267, 21894* (19) - **F.C. Hoehne** *29972* (3); *5998* (7); *20294* (9) - **M. Hoff** *5199, 5694* (7) - **B. Hoffman** *409* (9) - **L.R. Holdridge** *1945* (4a); *1738* (9) - **K. Holl** *1050* (17) - R.**W. Holm** *728* (4a); *728* (5) - **W.C. Holmes** *4269* (10) - **L. Holm-Nielsen** *4543* (3); *19624, 20469* (9); *24430* (10); *20385*

(17) - **B.K. Holst** *2300* (3); *7135* (5); *9002* (10); *9069* (13) - **E.W.D. Holway** *1148* (7) - **J. Hoock** *82, 89, 90, 93* (7); *83, 91* (9) - **M.J.G. Hopkins** *782* (2); *#79* (9) - **Bro. Horam** *2240* (16) - **F.W. Hostmann** *13, 511* (7) - **N. Hotchkiss** *6460* (4a) - **P. House** *993* (10); *1238* (17) - **R.A. Howard** *384, 8672, 9503, 10069, 11100* (4a); *9454, 11276, 12237, 14990, 19888* (9); *6250, 9508* (18) - **O. Huber** *4786* (9) - **J. Hudson** *885* (3) - **M.J. Huft** *2373* (10); *1667* (19) - **Humbert** *27605* (4a) - **F.W. Hunnewell** *15224, 20116* (4a); *18805* (9); *17091* (10); *16395* (11a); *16394* (13); *15226* (18) - **D.R. Hunt** *5673* (9); *268* (13); *266* (15) - **A.A. Hunter** *760* (9) - **T. Husnot** *93* (4a); *94* (9) - **A. Ibáñez** *1516* (9) - **T. Ibarrola** *4054* (9) - **J.M. Idrobo** *2176* (9); *4274* (13) - **H.H. Iltis** *313* (7); *130* (9); *86, 44, 128* (10); *349* (13); *86* (14); *1620* (16) - **R.R. Innes** *RRI 58* (4a); *59* (5); *49* (15); *92* (16); *74* (18) - **Intosh** *3* (4a) - **H.S. Irwin** *54540, 55790* (2); *12268, 13958, 14155, 23138, 24237, 28160, 55790A, 57618* (7); *5624, 7030, 15453, 21180, 23138, 28160, 31599* (9) - **J.G. Jack** *4380* (4a); *7053* (9); *5187* (18) - **D. Jackson** *134* (13) - **A.Jahn** *312* (3) - **J. Jangoux** *93* (7) - **J.P. Janovec** *2206* (7) - **M.J. Jansen-Jacobs** *163, 4149* (2); *1812, 2989, 3176, 5950, 6099* (7); *758, 966, 1274, 2182, 3346, 4149* (9) - **D.H. Janzen** *12241A* (4b); *s.n.* (4b); *12426* (13) - **R. Jaramillo-Mejía** *2753* (3); *1019* (13) - **J.G. Jardim** *2912* (3); *503, 871, 1115* (7) - **C. Játiva** *155, 889* (9) - **O. Jéllez** *1557, 1799* (4a) - **G.S. Jenman** *35* (6); *257, 1916, 2053, 3593, 4089* (7); *256* (9); *813* (13) - **J. Jeremie** *193* (4a) - **B. Jestrow** *2012-018, 2012-429* (4a) - **A. Jiménez** *1271* (14) - **B. Jiménez** *1379* (9) - **M. Jiménez** *31045* (13) - **O. Jimenéz** *378* (4b) - **F.W. Johnson** *1246* (2) - **I.M. Johnston** *1078, 1272* (9); *904* (11a); *442* (13); *1255* (16); *548* (17) - **M.C. Johnston** *6028* (10); *5754, 12243* (16) - **G.C. Jones** *3054, 3474* (16) - **M.E. Jones** *27414* (10) - **S. Jones** *5385* (10) - **H. Jorgenson** *1119* (17) - **A. Juan** *13* (17) - **E.J. Judziewicz** *4283* (9); *4377* (10); *4295* (14) - **S.L. Jung-Mendaçolli** *562* (3) - **G. Jürgens** *6391B* (9) - **A. Kappler** *s.n.* (7) - **V. Kapos** *1606* (9) - **Karsten** *s.n.* (10) - **R. Kayap** *903* (7); *744, 1096* (9) - **H.A. Keller** *2100* (16) - **W.A. Kellerman** *7472* (9); *4735* (10); *7486* (11a) - **H. Kennedy** *677* (4b); *677, 1398* (10) - **E. Kerber** *74* (4a); *74* (10) - **R. Kiesling** *5644* (9) - **T. Killeen** *883, 2099, 2332, 6308* (9) - **E.P. Killip** *16794, 25615* (3); *13509, 32037, 42259* (4a); *13528* (5); *23080, 25255, 26327, 27125, 27561* (7); *5052, 9732, 14681, 14992, 16302, 20901, 23998, 28673, 30674, 34837, 37030, 37706, 38230* (9); *5444, 8770, 11649, 17013* (10); *4284, 25170* (11a); *5366, 11564, 12066, 34505* (13); *11607* (14); *4040, 14082, 14126, 14513,16476, 38261, 44165, 44533* (16); *33554, 33594* (17); *19411* (18); *4529, 6149, 7714, 8259, 33774, 10138* (19) - **M. Kimnach** *2022* (16) - **R.M. King** *1057, 4813* (10); *4802* (13); *4925* (16) - **W. Kings** *166* (4a) - **J.H. Kirkbride** *2764* (7); *1931, 2223* (10); *90* (13); *1553* (17); *2496* (18) - **R.M. Klein** *2026, 8089, 11735* (3); *1320* (7) - **B.B. Klitgaard** *517* (16) - **G. Klug** *4372* (9) - **S. Knapp** *2723* (4b); *4869* (9); *5623* (10); *1241* (16); *4383* (19) - **S.D. Koch** *78244* (5); *82171* (10); *78235* (13); *79302* (16) - **Køie** *5237* (4b); *5311* (9) - **T. Koyama** *14098* (11a); *7500* (13) - **L. Kollmann** *6048* (3) - **R. Kral** *49192, 57134* (4a) - **A. Krapovickas** *23624, 32064, 34930, 41058* (9) - **W.J. Kress** *94-3973* (10) - **J.G. Kuhlmann** *2002, 152952* (7) - **J. Kuiper** *27915* (18) - **O. Kuntze** *s.n.* (3) - **L.P. Kvist** *305* (7) - **S. Lægaard** *18533, 18927, 19171, 51912, 53405, 53395, 54202, 54711, 71372, 101029, 101083* (3); *17656, 18895, 51503, 55837, 102469* (7); *20237, 52077, 52471, 53994, 54712, 54713, 57466, 55839, 70782, 70774, 71223, 71257* (9); *70821, 18630, 18919, 19099, 19171, 20856, 53395, 55479* (10); *19171* (13); *54629* (17); *71243, 71248* (18) - **H. Lainez** *173* (4a) - **L.R. Landrum** *10611* (7) - **E. Langlassé** *556* (11a); *540* (13); *458* (16) - **J. Lanjouw** *1384, 2146* (7) - **J.P. Lanna** *568* (7) - **M.E. Lara** *60* (10) - **A. Lasseigne** *4966* (16) - **T. Lasser** *665* (10); *1534* (13) - **E.W. Lathrop** *5580* (9); *6006* (13); *5522* (17) - **R.M. Laughlin** *1218, 1572, 2289, 2553, 2807* (10); *277* (16) - **A.E. Lawrence** *219* (3); *795* (13) - **R.L. Lazor** *2945* (10) - **C. Leavenworth** *1255* (13) - **W. Leavenworth** *1901* (16) - **J.M. Leeuwenberg** *11763* (2) - **C. Le Gallo** *549* (4a) - **K.R.B. Leite** *315* (7) - **R.W. Lent** *1736, 3981* (10); *2154* (13) - **Bro. León** *767, 2602, 12777, 14118, 17336* (4a); *10666* (5); *12462* (15); *3778* (16); *5148, 13171* (18) - **J. Léon** *1702* (13); *2926* (16) - **León de la Luz** *4070, 12294* (4a) - **E.C. Leonard** *2907, 3071, 3072, 3081, 3785, 4950, 7910, 8249, 9007, 9293, 11116, 11235,* (4a); *3670, 3976, 7158, 7776, 7810, 8475, 9042, 9282, 9352, 9668, 11563, 14197* (9); *7997, 8192, 8572, 9391* (11a); *3240, 5054, 5121, 7650, 9466, 14292* (18) - **J. Leonel Salguero** *11* (10) - **F.M.R. Leprieur** *s.n.* (7) - **E. Lewis** *CEL 02-060* (5) - **M. Lewis** *88843* (9) - **W.H. Lewis** *7476* (4a); *569* (10); *2594* (11b); *244* (12); *2301* (13); *3328* (16); *3376, 12106* (17); *2896* (19) - **J. Lezcano** *330* (19) - **N. Lezcano** *26* (16) - **F.M. Liebmann** *6308* (4b); *289* (9); *6317* (10); *14195* (13) - **R. Liesner** *5532, 11882, 12026* (2); *4229, 26611* (4b); *1483* (5); *17412, 21608* (7); *267, 5459, 10320* (9); *11694, 26580* (10); *64, 1588* (11a); *9256* (13); *4422* (16); *267A, 1988* (17); *527* (19) - **J. Lima** *774* (2) - **C.A.M. Lindeman** *s.n.* (3); *1239* (7) ; *1701, 3185b* (9) - **J.C. Lindemann** *619* (2); *929, 6198, 6933* (7); *158, 336, 1547, 4290, 13301* (9) - **J.J. Linden** *1948* (13) - **M. Lindig** *1044* (9) - **A.H. Liogier** *9899, 12410, 15917, 16944, 17049, 17367, 18839* (4a); *10418, 32736, 33832, 35847* (7); *18799, 24732, 26054, 37301, 38886* (9); *17049* (18) - **E.M. Lira** *C. 604* (4a); *368* (15) - **Lister** *103, 187* (7) - **E. Lleras** *P17333* (7) - **S. Lobo** *218* (17) - **L.G. Lohmann** *465* (7) - **B. Løjtnant** *14986* (10) - **X. Londoño** *177* (3); *830* (4a); *14, 616* (7); *283, 373, 547, 613* (9); *56* (10); *145, 459* (13) - **E.M. López** *3072* (9) - **J.E. López Contreras** *1083* (16) - **L. López** *547* (9) - **E. López Garcia** **56** (10) - **R. López Luna** *493* (10); *338* (13) - **A. Lot** *1102* (9); *4003* (16) - **A. Loureiro** *38879* (7) - **K.S. Lowell** *488* (9) - **S.R. Lowrie** *185* (7) - **R. Lozano** *1275* (9); *1922* (10) - **H. Lugo** *2357, 2497, 4114, 4985, 5211, 5311* (9); *2497* (16) - **A. Luna** *206* (4a); *1007* (9) - **C.L. Lundell** *1587, 12405, 20292, 2332, 3548, 6430* (4a); *6751, 16144, 16360, 16665* (5); *16983* (9); *6434, 19598* (10); *17788* (11a); *6571* (13); *91, 550, 918, 6840, 15531, 15713, 16106, 17145* (15); *3862, 16106, 17240* (16); *555, 904, 16146* (18) - **J.L. Luteyn** *4799* (9); *10396, 12548* (10); *1687* (13) - **B. Lutz** *1374* (7) - **E. Lyonnet** *2658* (16) - **J.M. Maarten** *5568* (10); *5426* (19) - **P.J.M. Maas** *7150* (2); *6966, P13109* (7); *7150* (9); *1635* (10); *1132* (13) - **J.S. McCorkle** *C-126* (11a); *199* (13) - **S. McDaniel** *11097, 16411, 16566* (7); *10048* (8); *8178, 17368* (9); *10158* (10); *5121* (12); *23266* (13); *14732* (16) - **J.M. McDougal** *3368* (4a); *3757* (9); *3463* (10); *3240* (13); *3125* (18) - **T. McDowell** *1889, 2424, 4365* (7) - **R.L. McGregor** *933* (18) - **H.S. McKée** *11182* (9); *11284* (10); *11101* (11a); *10955* (16) - **P.M. McKenzie** *781* (4a) - **G. McPherson** *1133* (8); *7179, 7220, 11692, 15958* (10); *7459* (12); *11298, 11499* (13); *6981, 6987, 10246* (17); *8290, 8442, 10289A* (19) - **McRee** *10956* (4a) - **R. McVaugh** *360, 828, 13306, 14232, 17363, 19756* (10); *510, 21157* (11a); *500, 13357, 19101, 20165, 21152* (13); *722, 1498, 17925, 18051, 19975, 20761, 21022, 21144, 25036* (16) - **A. Macedo** *3734* (9) - **G.E.L. Macedo** *41* (3) - **E. Madrid** *292* (18) - **B. Madrigal** *679* (9) - **J.E. Madsen** *7085* (10) - **B. Maguire** *27275* (2); *23965, 24746, 53806* (7); *33758* (10); *32663, 45951A* (13) - **G. Malme** *3357* (7) - **O. Malme** *A.3185b* (9) - **B.N. Manco** *14* (4a) - **S. Madriñan** *513* (13) - **M. Manna** *2* (4a) - **G. Manzanero** *1141* (10) - **Marcano** *3371* (9) - **G. Marín** *146* (9) - **S.A. Marshall** *6608* (16) - **S. Martén** *656* (14) - **R.F. Martin** *1281* (4a) - **M.A. Martín Ballestreros** *MB127* (2) - **Martínez** *34872* (11b); *34852* (12); *31463, 31503, 35000* (15) - **E.M. Martinez S.** *16949, 23363* (4a); *7362, 7725, 8247, 15381, 29360, 31555* (5); *13218* (8); *35169* (11a); *2960* (15); *1359, 31694* (16); *27983, 35679* (18) ; *17189, 34787* (19) - **F.M. Martinez** *2182* (16); *F-2102* (18) - **G. Martinez-Calderón** *483* (11a); *239* (13) - **G.M. Martinez** *45* (12) - **L. Martorell** *546* (9) - **M.E. Mathias** *3463* (7); *3463* (17) - **S.**

Matthias *186* (13) - **L.A. Mattos Silva** *537, 1007, 1101, 3489* (7) - **E. Matuda** *3242* (4a); *3987. 26752* (10); *17286* (11a); *1939* (14); *2117, 3292* (16) - **H. Maturo** *282* (9) - **W.R. Maxon** *473, 10463* (4a); *8050* (9); *128, 7998* (10); *4653, 5266* (11a); *7546* (16); *1673, 10502* (18) - **S. Mayo** *1024* (7) - **W. Meier** *16903* (3); *11205*, *16387* (9); *6212, 16899* (11a); *11168* (13); *15180* (18) - **M. Mejía** *6348, 7041*, *7842, 9974*, *23704*, *35528* (4a); *2753* (4b); *18396* (9) - **T.M. Mejia Ordonez** *36* (16) - **M. Melendez** *1066* (10) - **M. Mélinon** *s.n* (7); *397* (9) - **A. Mendez Ton** *4943, 5027* (4a) - **R. Mendez** *98* (10) - **J. Mendieta** *531, 689, 927* (13) - **J. Menjívar** *3616, 3624* (8); *3403, 3517* (10); *3404* (11a); *3482* (13); *3481, 3654* (14); *3691* (16) - **F. Mereles** *619* (7); *2717* (9) - **J. Merilainen** *36* (4a) - **M.J. Metzler** *37* (10) - **Y. Mexia** *5328, 7218* (7); *6725, 8233, 9252* (9); *6850* (10); *6581* (11a); *628* (13); *597, 8717* (16) - **J.T. Mickel** *1463, 1485* (13) - **Z. Mijango** *132* (13) - **Miller** *#B5* (4a) - **G.S. Miller** *1184* (7) - **J.S. Miller** *5998* (4a) - **O.O. Miller** *184* (2) - **W. Milliken** *326* (2) - **C.F. Millspaugh** *9132* (4a); *1968* (9) - **T. Miranda** *443* (3) - **K. Mizoguchi** *602* (7) - **B. Mogensen** *1143* (16) - **Mogg** *276* (2) - **H.N. Moldenke** *407, 3747* (4a) - **A. Molina** *18M.017* (3); *13291, 15628, 20845* (4a) ; *13894* (4b); *15503* (5); *205*, *16075, 27555* (8); *18 N.S. 070, 10566* (9); *76, 620, 1432, 11987, 10566*, *16067, 18494, 21108, 21605, 22361, 30671* (10); *3676, 16075, 25714* (11a); *11338* (11b); *18221, 14904* (13); *1433, 2766, 15446, 18651, 21091, 22013, 25824, 26149, 27483, 27554* (14); *15680, 30846* (15); *1085, 4051, 18651, 20662, 22466, 22858, 24610, 34262, 35161* (16); *17385, 18111* (17); *3541, 3814, 15818, 26229, 34261* (18); *10467* (19); *1811, 4051, 12880, 18631* (20) - **A. Monro** *153, 1018* (4a); *249, 1745, 2684* (5); *2194* (8); *409, 1987, 2194, 5827* (10); *2103* (11a); *1992* (14); *2267* (16); *4661* (17) - **O. Monsegur** *253* (4a) - **E.A. Montalvo** *6410* (10) - **J. Monterrosa** *222* (8); *918* (18) - **J.E. Montes** *68*, *15286*, *15401*, *27498* (3); *1592, 2198* (9) - **M. Montiel** *048156, 048157, 048158* (10); *20* (12); *20* (16) - **Montoya** *42* (12) - **H.E. Moore** *1951, 4235, 5076, 5598* (10); *5149, 5697* (13); *5107* (16); *5665* (16); *1328* (18) - **L.E. Mora** *2407* (10) - **C. Moraga** *686* (9); *914* (13) - **C.O. Morales** *414* (16) - **J. Morales** *4973* (4a); *1746, 3895* (8); *1673, 5654, 7065* (10); *7382, 10597* (13); *4947* (14); *6336* (16) - **R. Moran** *18223* (16) - **I. Morel** *2505, 5041, 7088* (9) - **P.P. Moreno** *12276* (4a); *19230* (5); *23302* (9); *25020* (11a); *11935, 17704, 22726* (13); *17603* (14); *18123, 27169* (16); *2673* (18) - **S. Mori** *16579, 17004* (4a); *10767, 22086* (7); *8486* (9); *5916* (10); *1731* (13); *4075* (16); *4881, 26723* (17); *5315* (19) - **G. Morillo** *4256* (16) - **B.D. Morley** *758* (6) - **T. Morong** *1569* (3); *641, 755* (9) - **O. Morrone** *670*, *1968* (3); *542, 1989, 2882, 4530, 4973, 5455* (9) - **C.V. Morton** *2914, 3433, 4143, 4528, 8753, 8879, 9972* (4a); *4276, 4306, 4390, 10198* (5); *6954* (8); *7633* (10); *2441* (16); *4441, 10194* (18); *7619* (19) - **H. Mosén** *s.n.* (3) - **B. Mostacedo** *105* (9) - **C.H. Muller** *2961* (10) - **P. Mutchnick** *354* (7) - **A. Mutinelli** *50* (3) - **E. Narvaez** *3356* (9) - **B. Nascimento** *606* (9) - **G.V. Nash** *1240* (4a) - **L. Nèe** *s.n.* (18) - **M. Nee** *47870* (2); *33770*, *44822*, *49193* (3); *3649* (4a); *47330, 25085* (5); *31755, 41359, 45215, 49530, 52814* (7); *8136, 8201, 8857, 9836, 10759*, *33436, 33617, 40568, 47330, 47905, 48671, 49200, 49591, 54974* (9); *18645, 24676, 32791*(10); *8853, 9124, 23843, 29907, 29773* (11a); *9616* (12); *6870, 7386, 7766, 24870* (13); *22602, 23073, 34030* (16); *9778* (17); *9295, 29937* (19) - **D. Neill** *5961* (3); *6840, 41680* (9); *2875, 4624* (16); *11562* (17); *2515* (18) - **C. Nelson** *3436* (9); *3648, 4034* (10); *4182* (13); *2087, 3021, 7474* (16); *2719* (17); *6654* (18) - **N.H. Nickerson** *2952* (4a) - **D.H. Nicholson** *28* (4a); *1893* (6) - **V. Nilsson** *536* (16) - **L.R. Noblick** *3180* (2); *3384, 4109* (7) - **A. Novelo** *30* (15) - **T.S. Nunes** *1213, 1222* (7) - **P. Nuñez** *7545, 11946* (10) - **L. Nusbaumer** *4257* (7) - **N. Obando** *136* (10) - **V.L. Ochoa** *161* (20) - **R.A.A. Oldeman** *B-3485* (7) - **F.C.A. Oliveira** *544* (9) - **R.P. Oliveira** *365* (3); *66, 737, 867, 1373, 1381* (7) - **R.S. Oliveira** *445* (7) - **J. Oliver** *2* (7) - **B. Øllgaard** *9260* (3); *35024* (7); *8994, 34583, 35473, 37710*, *53403* (9) - **C.R. Orcutt** *1488* (4a); *3544* (6) - **A.S. Ørsted** *14127*, *14128*, *14130* (4a); *14129* (4b) - **J.G. Ortega** *7058* (16) - **F. Ortiz** *20* (4a); *738* (11a) - **J.J. Ortiz** *559* (4a); *1087* (5) - **O.O. Ortiz** *1982* (4b); *516, 519* (9); *776, 1989, 2446* (10); *1757* (14); *2105* (17); *1988* (18); *783, 2026, 2303, 2348* (19) - **R.T. Ortíz** *326* (5); *2648* (15); *2171* (17); *204* (18); *1576* (19) - **S.L. Orzell** *23184* (4a) - **C.H. Ostenfeld** *55* (7); *s.n.* (9) - **J.I. Otero** *255* (4a) - **C.A. Padilla Gomez** *132* (14); *195* (16) - **G. Padilla** *48* (18) - **E. Palmer** *10, 362, 630, 27483* (4a); *535* (13); *10, 115* (16) - **M.R. Palmer** *3402* (4a); **W. Palmer** *s.n.* (4a); *1001* (18) - **J.L. Panero** *5060* (10) - **N. Paniagua** *Z. 1130* (7) - **L.R. Parodi** *4410, 4412* (9) - **C.C. Parry** *535* (13) - **R. Paz** *168* (16) - **T.M. Pedersen** *1717* (8); *4155, 5899* (9) - **M. Peña** *1055* (13); *554* (15) - **F.W. Pennell** *9621, 18014* (4a); *3225, 3237, 3916, 4605, 8567* (9); *3415, 5025, 7223, 7227* (10); *1648, 2870, 3777* (13); *18012* (18) - **E. Pereira** *5374* (9) - **J.M. Perla** *19* (4b) - **N.A. Perogolo** *365* (7) - **C. Perret** *532* (16) - **P.M. Peterson** *7560*, *7637* (2); *9533*, *15095* (3); *6517* (4a); *15034* (7); *6722, 6940, 7072, 9439, 15034, 15096* (9); *7382, 9533, 9819* (10); *6767, 7032, 7071 7312, 7377* (11a); *371* (13); *7369* (14); *9520* (16); *6711, 7102, 7110* (17) - **H.W. Pfeifer** *1447, 1879* (8); *1414* (10); *1622* (16) - **D. Philcox** *7906* (7) - **L.R. Phillipe** *21252* (9) - **Phillipson** *594* (4a); *1651* (13) - **M. Piepenbring** *1865* (16) - **M. Pignal** *1502* (7) - **G.E. Pilz** *1313* (10) - **J. Pimentel** *598, 1182* (4a) - **G. Pinto** *130/81* (2); *1105* (13) - **C.V. Piper** *5219, 5281* (9); *5288* (11a); *5948* (13); *5257* (16) - **J. Pipoly** *24740*, *24616*, *24820* (4a); *11301* (7); *24344* (10); *3786* (17); *16833* (19) - **J.R. Pirani** *2154* (9) - **J.M. Pires** *48844, 51007, 52353* (7); *852*, *1696a*, *52138* (9) - **H. Pittier** *10749* (1); 1650 (3); *1615, 2342* (4b); *211, 1787, 2118, 2196, 4455, 7110, 6384, 9893, 14968, 11770* (9); *886, 5331* (10); *2247, 15209* (11a); *5422* (11b); *3114* (12); *1645, 6774, 8059, 11854, 12057* (13); *1616* (14); *4688, 4998, 7686, 10617* (16); *9492* (17); *875, 5339* (19) - **T.C. Plowman** *7251* (7); *9047* (9); *7558* (11a); *2246* (13) - **E. Poeppig** *s.n.* (5) - **R.W. Pohl** *9991* (4a); *11406, 13826, 13834, 14136* (4b); *13410* (5); *14135* (8); *10790*, *11365* (9); *10070, 10280, 10310, 10388, 10870, 10889, 11041, 11050, 11134, 11166, 11174*, *11198, 11214, 11250, 11275, 11351, 11371, 11403*, *11477, 13250, 13594, 13661, 13796, 15567* (10); *11522*, *13121, 13827* (11a); *11522* (11b); *10829* (12); *10016, 10356, 10824, 10960, 10993, 11055, 11096, 11163* (13); *10994, 11179, 11481, 11694* (14); *9826, 10048, 10161, 10192, 10541, 11278, 11335, 11562, 12583, 13424* (16); *10791, 11692* (17); *10300*, *10832, 10994, 11123, 12637* (18); *11675* (19) - **J. Polanco** *2013* (13) - **C.L. Pollard** *76, 157* (4a) - **O. Poncy** *1128, 2890* (7) - **F.W. Popenoe** *47* (9); *32, 735* (11a) - **O. Porsch** *180* (10) - **D.M. Porter** *4271* (17) - W.**Z. Pounds** *270* (10); *74* (11a) - **D. Prado** G. *95* (13); *276* (17) - **J. Prado** M. *223* (11a) - **G.T. Prance** *1823, 4311, 5158, 5954, 6451, 8926, 13723, 25017, 58699* (7); *10052*, *15832* (13) - **M.F. Prévost** *787, 1969* (7) - **C.G. Pringle** *3808, 6663, 6701* (10); *1732* (11b); *1732, 11760* (13); *11293* (16); *3403, 3808* (18) - **G.R. Proctor** *7108, 7315*, 17221, *20298*, *29244* (4a); *29866* (5); *9585*, *23405*, *23834, 25592* (6); *9626, 16025*, 17293, *24243, 29244, 33008, 42704* (9); *105* (11a); *29865* (15); *27281* (17); *38265* (18) - **G. Proctor Cooper III** *26* (9) - **J. Pruski** *1534* (4a) - **H. Puig** *5167* (10) - **A. Pulle** *227* (9) - **C.A. Purpus** *2905* (4a); *6206* (9); *3779, 5440* (10); *2157* (11a); *7813* (13); *5438* (15); *5978* (16) - **C. Quarín** *3388* (9) - **C. Quelal** *264* (9) - **G. Quenette** *35* (7) - **F. Quesada** *279* (17) - **J. Quesada** *928* (4b); *1646* (10); *901* (16) - **A. Questel** *600, 845, 4023, 4646* (4a) - **L. Quiñones** *982* (9) - **V. Quipuscoa** S. *316* (9) - **W. Quizhpe** *857* (9) - **G. Raddi** *s.n.* (7) - **Rafael** *1686* (19) - **G.A. Ramage** *s.n.* (6) - **B. Rambo** *40005*, *46452*, *47132* (3); *53497* (9) - **L. Ramella** *LR2501* (9) - **M. Ramia** *8779* (7) - **E. Ramirez** G. *391* (4a); *98* (10) - **F. Ramírez** *1570* (13) - **M. Ramírez** *105* (10) - **N. Ramírez** *2769* (2) - **V. Ramírez** *2231* (10); *59* (11a); *248* (19) -

Ramon de la Sagra *16* (4a); *44* (18) - **H.J. Ramos** *187* (12) - **J.E. Ramos** *2706, 2909* (9); *984* (10) - **J.A. Ratter** *1998* (7); *939, 2120* (9) - **C. Raunkiaer** *642, 951* (4a); *642, 2304* (7) - **A.M. Raynal** *15598* (9); *19643* (18) - **J. Rebman** *29186* (4a); *32016* (16) - **K.M. Redden** *2184* (7) - **J.R. Reeder** *4765* (10); *2137, 2156, 2373, 2399, 2423, 4156, 4333, 6345, 6346* (16) - **R.D. Reeves** *209* (7) - **A.F. Regnell** *308* (3); *308* (7) - **A.L. Reina** *124* (13) - **P.R. Reitz** *3775, 7079* (3); *2951, 8292* (7) - **B.P. Reko** *3474* (10) - **S.A. Renvoize** *4024* (3); *4744* (9); *4045, 5370* (10); *5364* (19) - **J.L. Reveal** *4020* (10); *4043* (13); *4020, 4061* (16) - **J. Revilla** *2136* (13) - **A. Reyes-García** *2227* (4a); *1491, 1895* (4b); *2460* (5); *1147* (9); *1023, 5204* (10); *1278* (12); *7284* (13); *1147* (16); *969, 1414* (18) - **C. Reynel** *5032* (7) - **O.S. Ribas** *1326* (3) - **P.W. Richards** *6531* (7) - **L. Richey** *98-246* (4a) - **L. Rico** *1177a* (4a); *1177b* (10); *1177c* (15) - **H.N. Ridley** *24* (9); *27* (11a); *35* (18) - F. **Riedle** *s.n.* (4a) - **L. Riedel** *s.n.*, *218*, *963* (7); *1239* (13) - **R. Rimachi** *11761* (3); *5155, 5634* (7); *1148, 5634, 11045, 11452* (9) - **P. Rios** *80* (12) - **E. Ritter von Friedrichsthal** *1539* (4a) ; *549* (9); *549* (13) - **J. Rivera** *1847* (16) - **Robert** *332b* (7) - **Robertson** *s.n.* (4a) - **W. Robleto** *1711* (11a); *1494* (11b); *62A* (16) - **M.J.N. Rodal** *1325* (7) - **A. Rodriguez** *11939* (9); *11956* (10); *4896* (11a); *1801* (16) - **D. Rodriguez** *272* (10); *158, 649* (16); *3300* (20) - **E. Rodriguez R.** *1244* (7); *64* (16) - **L. Rodriguez** *1777* (10); *1235* (14) - **V. Rodriguez** *3422* (16) - **K. Roe** *767, 1903, 2207* (10); *1367* (13); *1432* (16) - **R. Romero Castañeda** *9096* (16) - **R. Rojas** *5738* (7); *739, 2869* (9) - **N.A. Rosa** *3388* (7); *3193* (13) - **M. Rosas** *830* (10) - **J.M. Rosales** *543* (4a); *1495, 1870* (16) - **J.N. Rose** *3660, 3739*, *4159* (4a); *3484, 3624* (9); *14459* (10); *23525* (11a); *3502* (16) - **Rouselle** *GU96/106* (7) - **W.W. Rowlee** *945* (13) - **P. Ruben** *8418* (4a) - **D. Rubio** *1776* (9) - **R. Rueda** *2608* (4a); *3355, 15294* (9); *15225*, *17748* (11a); *9639, 16543* (13); *12891, 17662* (16); *2745, 3246* (17); *10699, 16351* (19) - **N.P. Rugama** *26* (16) - **F. Rugel** *111* (4a); *187* (5); *868*, *872* (18) - **H.H. Rusby** *191, 358* (9); *861* (10); *516* (13) - **D. Russell** *31* (4a); **G.F. Russell** *769* (9); *769* (11a); *769* (17) - **R.A. Russell** *9388* (9) - **J. Rzedowski** *14254, 26926* (10); *17844* (13); *17729, 17880, 17932* (16) - **F.M. Saavedra** *13* (14) - **J.L. Sadle** *#115* (4a) - **J. Saer d'Héguert** *280* (18) - **P.A. Sagot** *656* (7) - **S.H. Salas** *4213* (16) - **A.E. Salazar** *31* (13) - **M. Saldias** *4348* (3); *5029* (9) - **J. Salick** *7319* (9) - **M. Salzmann** *s.n.* (7) - **F. Sánchez** *170* (9) - **J.G. Sánchez-Ken** *672* (4a); *678* (12); *679* (19) - **I. Sánchez Vega** *9429* (9) - **A.C. Sanders** *11266* (10); *10476* (11a); *10349* (13); *17582* (16) - **R.W. Sanders** *1851*, *1881* (4a) - **J.C. Sandino** *1584* (14); *4283* (19) - **E. Sandoval** *ES-01763* (4a); *13* (10); *1467* (11a) - **D. Santamaría** *761* (17); *7441* (19) - **S. Sant'Ana** *996* (7); *775* (9) - **F.J. Santana** *5241, 5369* (10); *5494* (13); *2261, 2960* (16) - **J.V. Santos** *2269* (4a); *2650* (5); *3076, 3347* (10); *2500* (13); *2269* (15); *3534* (16) - **N.Y. Sandwith** *s.n.* (7); *1322* (13) - **C. Sargent** *295, 3236* (4a); *10114* (9) - **A.C. Sarmento** *743* (2); *888* (7) - **C.H.L. Sastre** *7036, 7157* (4a); *2539, 4258* (9); *629* (13) - **R.P. Sauleda** *1579* (4a) - **J. Saunders** *881* (4a); *1216* (9); *700* (13) - **J. Schenck** *2947* (3); *3754* (7) - **M. Schessl** *3410* (9) - **R.A.A. Schnell** *11692* (7); *11692* (9) - **A. Schinini** *6103*, *15187, 16582, 23773*, *28045* (3); *4728, 6200, 14045, 28066, 28255,* (9) - **W.A. Schipp** *332* (4a); *1276* (5); *1368* (11a); *785* (13) - **B.G. Schubert** *1137* (17) - **H.E. Seaton** *393* (10) - **P.J. Shank** *4755* (12) - **R.E. Schultes** *6006* (9) - **Schulz** *10464* (2) - **J. Schunke-Vigo** *12146* (3); *1938, 2618, 7559, 10089, 12146, 16181* (7); *6138, 7467, 8241, 9550, 10214, 11669* (9); *7001, 9758* (11a); *2989* (13) - **G.J. Schwarz** *2290, 2542, 10232* (3); *2290* (9) - **E. Schwindt** *42, 119, 297* (9) - **R.S. Secco** *331* (7) - **R.J. Seibert** *628* (13) - **R. Seidel** *7793* (3); *2089, 2463* (7); *1185, 7813* (9); *2155* (18) - **W. Seifriz** *165* (13) - **E. Seler** *2446* (16) - **T. Sendulsky** *665* (3); *1990* (9) - **A. Sermeño** *33* (4b); *33* (16) - **M. Serrano** *4917* (3) - **F.C. Seymour** *3840* (4b); *845, 2831, 3841* (16) - **J.A. Shafer** *700, 1073, 2549, 2571, 3017, 7827, 8751, 10597, 13564* (4a); *12006* (5); *701, 2570, 12323* (9); *11684* (16); *11147* (18) - **O.E. Shattuck** *528* (9); *528* (13) - **M. Short** *222* (10); *185* (17) - **K. Sidwell** *407, 887* (10); *411, 819* (14); *610* (16) - **R.J. Siebert** *278* (8) - **A.D. Skelding** *3481* (9) - **L. Skog** *7106* (7); *7106* (9) - **A.F. Skutch** *2189, 3817, 3875, 3876*, *4392, 4631* (9); *986, 3148, 4397* (10); *3821, 3863* (11a); *2226* (11b); *3862, 4040, 4655* (12); *1298, 2167* (13); *2155, 3871, 5391* (17); *1345* (18); *2206, 3674, 3680, 3802, 4460, 4571, 4649* (19) - **A. Silva** *168* (7) - **B.M. Silva** *2247* (7) - **J.A. Silva** *473* (2) - **M.N. Silva** *214* (9) - **M.M. Silva-Castro** *1027* (7) - **F.A. Silverstone-Sopkin** *3396* (9); *7266* (10); *7401* (11a); *5913* (18) - **M.F. Simon** *1564* (7) - **D.R. Simpson** *8* (5); *423* (9); *658* (13) - **P.E.E. Sintenis** *68, 2318*, *2470* (4a); *215, 5918* (7); *215, 2861, 3062* (9) - **V. Slane** *121* (9) - **D. Sloot** *354* (10); *217* (14) - **J.K. Small** *64, 2133, 2864, 3947, 4647*, *7345*, *8586, 8771* (4a) - **A.C. Smith** *10200, 10306* (4a); *3314, 3131, 10199* (9); *41015* (10) - **D. Smith** *1852, 2145* (9) - **D.N. Smith** *4026, 6991* (7); *4050* (9) - **H.H. Smith** *1976*, *3131* (2); *2144*, *2148* (3); *909*, *2417*, *4071*, *13637* (7); *2147, 2148, 2258, 2531* (9); *2144* (10); *2142* (11a); *117* (13); *174* (16); *2417* (17); *2145* (18); *2148, 2258, 4407, 6806* (19) - **J.D. Smith** *3906* (13) - **L.B. Smith** *11783* (3); *3269* (4a); *2284, 6039, 6335* (7) - **M.L. Smith** *753, 888* (4a); *1710* (11a) - **S.F. Smith** *909* (7) - **S.G. Smith** *1295* (9); *1534* (18) - **S.C. Snedaker** *D 51* (16) - **G.L. Sobel** *2155* (10) - **T.R. Soderstrom** *1126* (2); *1927* (3); *1036, 1071, 1198*, *1415, 1872, 1948, 1957, 1976, 2132, 2190* (7); *974, 1357* (10); *2012* (12) ; *469, 611, 1212, 1402* (13) ; *2007* (19) - **S.H. Sohmer** *9683* (9) - **E.R. Sohns** *1590* (4a); *1689* (5) *1617* (9); *286, 1198, 1378, 1390* (10); *1685* (11a); *864* (13); *966, 1408, 1417* (16); *1406* (18) - **D. Solano** *5213* (8); *4709* (10); *5253* (19) - **J.C. Solomon** *9879*, *12020* (3); *5714* (4a); *3240, 16698, 17024* (7); *1394, 1407, 1413, 6297, 6863, 14088* (9) - **R. Soreng** *2185* (16) - **A. Soto** *112, 1463* (10) - **J.C. Soto** *23139* (5); *13327* (11a); *75, 11337, 11346, 13209* (16); *23284* (18) - **J. Soukup** *3022* (17) - **R. Souza** *159* (3); *427, 840, 10115* (7) - **D. Soza** *295* (9) - **B. Sparre** *15516, 16128* (9); *17983* (11a) - **M. Sparrow** *27* (10) - **R. Spellenberg** *4596* (16) - **D.L. Spellman** *1713, 1598* (4a); *559* (13); *1661* (18) - **C.R. Sperling** *5771* (7) - **Splitgerber** *446* (7) - **R. Spruce** *(17), (23), 412, 795, 1099* (7) - P.**J. Stafford** *138* (10); *154* (13) - **A. Stahl** *7* (7) - **G. Stahel** *2854* (2) - **P.C. Standley** *24889, 54545, 72832, 85472* (4a); *19136*, *19878, 62204, 75416*, *79364* (4b); *86936* (5); *23126* (8); *23117, 25955, 25987, 26065, 26651, 28142, 28320, 29523, 32022, 39648*, *40837, 41296, 41665, 43476, 47060, 46876, 47168, 62914* (9); *21508, 26837, 33365*, *39215*, *47507*, *49448, 57903, 60762, 62918, 63194, 68268, 81531, 82866, 87067, 87968* (10); *24122, 24910, 26009, 28535, 30230, 31609, 45151, 58104, 76153* (11a); *44523* (11b); *23712* (12); *20512, 23576, 24244, 27055, 62914, 79136* (13); *23109 a*, *440071, 44236, 45498, 86730* (14); *91779* (15); *15177, 19421, 19870, 20109, 20660, 21138, 22316, 26077, 26693, 27870, 30807, 44888, 46695, 52803, 62085, 74114, 74531*, *76224, 77080, 79009, 88381* (16); *37178, 45897* (17); *45532, 45820, 49785, 50068* (19); *12728, 22316, 23373, 23574, 24173, 24859, 26683, 26686* (20) - **L.R. Stanford** *870, 2502* (10); *1061* (18) - **M.N.S. Stapf** *828*, *844, 860, 861, 862, 917, 918, 919* (9); *813, 847, 849, 858, 867, 871, 872, 874, 875, 878, 897, 900* (10); *904, 915* (11a); *854, 856, 878, 898, 899, 911, 913* (11b); *799*, *810, 820, 921* (12); *791, 841, 843, 902, 919, 920, 940* (13); *855, 856, 873, 876, 877, 896, 903, 905* (14); *907, 908, 909* (16); *815, 939* (18); *554, 795, 804* (19) - **H. Stehle** *2607, 2086* (4a); *1945, 5436* (9) - **B.A. Stein** *1376* (11a); *1134* (12); *1149* (19) - **J. Steinbach** *9091* (3); *7111* (9); *8976* (10) - **V.W. Steinmann** *1913* (16) - **B. Stergios** *5876* (2); *19993* (10) - **W.L. Stern** *342* (9); *2032* (10); *1865* (16); *851* (17) - **W.D. Stevens** *17811* (4a); *16320* (4b); *16500*, *25907* (5); *2259, 7214, 24108* (9); *14103, 25492, 25750* (10); *21238, 27794* (11a); *11474* (11b); *18061, 22444*, *25234* (13); *16212, 23104* (14); *25220* (15); *13237, 22424* (16); *6390* (17); *6708, 11373* (19) - **W.C. Steward** *P12839* (7) - **J.A.**

Steyermark *41967*, *123600* (1); *57686, 88215, 107854, 108 440, 110955, 113905* (2); *91783*, *103639* (3); *45305* (5); *116550, 121318, 131009* (7); *47347*, *43405* (8); *45402, 12799, 61869, 118776, 88188, 90036, 91813* (9); *37137, 42603, 46406, 47982, 48627, 52868, 55106, 56098, 92125, 99450, 111910-A, 118178, 120079, 120152* (10); *116381, 124922* (11a); *42250, 49201, 61115, 89542, 107806-A, 126948, 127004* (13); *29294, 30083, 51810, 120268* (16); *88189* (18); *104658, 105551* (19); *92125* (20) - **W.R. Stimson** *3193*, *5188* (4a) - **A.L. Stoffers** *1184* (4a); *238* (7) - **H.E. Stork** *2577* (10) - **R.M. Straw** *2450* (7) - **J.J. Strudwick** *4176* (7) - **T.F. Stuessy** *4140* (16) - **D. Sucre** *2752* (3); *2098*, *6555, 10743* (7); *123* (16) - **A.M. Sugden** *1123* (9) - **L. Suin** *1266* (9) - **G. Sullivan** *1120* (9); *634* (13) - **D. Sutton** *299* (18) - **J.R. Swallen** *4419*, *4516* (2); *3773*, *8959* (3); *2452, 2489*, *2512, 2625, 2641*, *2706*, *2897, 5200, 5248, 10694* (4a); *2750, 2823* (5); *5051, 8756, 9005* (7); *10900, 11138* (8); *1947*, *3623*, *3888, 4354, 8756, 30153* (9); *10904, 10973* (10); *10970, 11303* (13); *10903* (14); *2445, 2518, 2665, 2677, 2696, 2697, 2698, 2713, 2716, 2761, 2824, 2879, 2887, 2902* (15); *2396, 2398, 2418, 2635, 2694, 2717, 2808, 11008* (16); *2415*, *2519, 2714, 2807, 2817* (18) ; *11008* (20) - **K. Systma** *3188* (9); *2901, 4358* (12); *1062* (13); *3055* (17); *3531* (19) - **J.Y. Tamashiro** *1181* (3) - **F. Tamayo** *2010* (20) - **E. Tameirão Neto** *439* (9) - **W.R. Tate** *364* (4b) - **T. Tateoka** *1031* (8); *1002* (9); *1003, 1004* (10); *1030* (14); *1001* (16) - **C.M. Taylor** *8138, 9481, 9508* (4a) - **J. Taylor** *18156* (9); *11866* (10); *17404* (11b); *18043* (16) - **N. Taylor** *328* (18) - **R.J. Taylor** *4471* (4b); *4520* (13); *4577* (14) - **L.O.A. Teixeira** *104.091, 104565* (7) - **O. Téllez** *9882, 12194 (*10); *12998* (13); *3940, 4330* (14); *3021, 3669* (15); *3368, 10788, 12323, 12462* (16) - **P. Tenorio L.** *3483* (4a); *3503, 6890* (10); *15802, 16092* (13); *2725, 14739* (16) - **H. Teppner** *316* (9) - **C. Thiébaut** *371* (4b) - **C. Thieme** *5585* (11a); *5585* (16) - **W. Thomas** *4490, 9927, 9982, 10027, 11431, 11570* (7); *10027, 10636, 11423 b, 13691* (9); *6682* (10) - **S.A. Thompson** *385, 7798*, *9777, 11378* (4a); *8230* (9) ; *4690* (17) - **S.S. Tillet** *738-549* (18) - **M. Timaná** *712* (7); *705* (9); *1907* (17) - **G. Tipaz** *803* (16) - **S. Tiwari** *462* (7) - **A.M. Ton** *4609* (14) - **A.S. Ton** *1183, 1446, 1582* (10); *1653, 3077, 3294* (13); *3180, 3269* (16) - **A.Tonduz** *7234, 9492* (4a); *13748* (4b); *12858, 13755* (9); *7207, 7234* (10); *7199, 12858 bis* (11b) ; *8186, 11397* (12); *9213* (17) - **R.A. Toro** *377* (9) - **R. Torres C.** *1915* (4a); *11473* (5); *12581* (9); *11549* (11a); *16788* (16) - **O. Tostain** *1683* (7); *1128* (9) - **O. Tovar** *4141, 4144* (16) - **S.M. Tracy** *9050*, *9094, 9320* (4a) - **S. Tressens** *6108* (3) - **M. Troetsch** *22* (9) - **S. Tsugaru** *B-729* (7) - **J.M. Tucker** *693, 733* (10); *694* (11a); *777* (13); *488* (16) - **R. Tún Ortíz** *1598* (11a) - **T.G. Tutin** *412* (9) - **E.L. Tyson** *5666, 5802* (8); *3078* (9); *5061, 5070* (11a); *2422* (12) ; *1378, 1689, 6656* (13); *1806, 3096, 5150, 6028* (16); *2598, 3327* (17) - **E. Ule** *4993, 8017* (7); *6225* (9); *8017* (16) - **L.M. Underwood** *252, 1642* (4a) - **A. Urbina** *181* (17) - **E.M. Urbina** *253* (9) - **J. Utley** *6424, 6463* (4a) - **E.J. Valeur** *s.n.* (4a); *307* (9) - **J. Valls** *2580* (3) - **F.M. Valverde** *6504* (11a) - **H. van der Werff** *7762, 9494* (9); *7316, 12172, 15616* (10); *4901* (13) - **Van Dolmen** *20* (18) - **Van Proosdij** *1025* (16) - **M. Vanilda** *130* (7) - **R. Vanni** *339, 3305* (9) - **J.D. Varela** *16* (9) - **C. Vargas** *14689* (7) - **H. Vargas** *746* (7); *6355* (10) - **I.G. Vargas** *2768* (9) - **M. Vargas** *342, 1051* (7) - **R.I. Vargas** *3746* (4a); *96* (5) - **Vásquez** *107* (15) - **B. Vasquez** *608* (4a) - **M. Vazquez Avila** *390* (9) - **M. Vasquez Torres** *2238* (18) - **R. Vasquez** *18647* (7); *18830* (9); *27196* (10) - **R. Vavrek** *64* (3) - **S. Vega** *19* (14) - **M. Velayos** *MV7033* (7) - **M. Véliz** *99.7712* (4b); *1586* (9); *14498* (10); *7024* (15) - **A. Veloz** *2097* (4a) - **Ventenat** *s.n.* (7) - **E. Ventura** *2300* (4a); *443, 2156, 2606* (16) - **W.C. Verboom** *5075* (4a); *5075* (8); *5035* (9) - **R. Villacorta** *2328* (4a); *2718* (14); *2324, 2693* (16); *2198* (18) - **P.C. Vincelli** *68* (16) - **M.A. Vincent** *#13300* (4a) - **J.L. Vivaldi** *338* (4a) - **P.C. Vogl** *944* (10) - **H.F.A. von Eggers** *2380* (4a); *6224* (9); *15572* (11a); *15553* (20) - **C. von Hagen** *1342* (5) - **G. von Langsdorff** *405* (7) - **H.W. von Rozynski** *589* (4b); *589* (10) - **K. von Sneidern** *164* (7); *164* (10) - **H. von Tuerckheim** *7696* (4a); *8623* (11a); *1481*, *8620* (12); *1028, 8781* (13); *715* (14); *809* (16) - **H. von Wedel** *1856* (9); *2086* (11a) - **R.L. Walker** *1244* (16) - **B. Wallnöfer** *5981* (15); *5958* (16) - **Walsh** *s.n.* (7) - **D.B. Ward** *3306, 5345* (4a) - **Warning** *s.n.* (4a) - **R. Wasum** *5961* (3) - **P. Weatherwax** *180* (4a); *94* (9); *180, 1715* (11a) - R.E. Weaver *1657* (12) - **H. Webber** *204* (4a) - **G.L. Webster** *9943* (2); *3832, 4058, 4998* (4a); *11898* (8); *31039* (9); *31039* (10) - **C. Weigelt** *s.n.* (7) - **A.L. Weitzman** *145* (10) - **K. Wendelberger** *398* (9) - **L. Werling** *517* (11a) - **F. Werner** *188* (10) - **J.G. Wessels Boer** *1158* (9) - **A.S. Weston** *2099* (13) - **D.A. White** *205* (16) - **C. Whiteford** *2024*, *2826*, *4486, 8269*, *10212* (4a); *1660* (4b); *2025, 106019* (5); *5163* (9); *1676* (10); *490* (11a); *114, 9331* (13); *2826* (15); *2138, 8163* (16); *214* (17) - **I.L. Wiggins** *430, 7148* (16) - **A.E. Wight** *118* (18) - J.T. Witherspoonn *8815* (4b); *8866* (10) - **R.L. Wilbur** *2556* (4a); *11289, 63341, 63701, 70209* (17); *10214, 11300* (19) - **J.R. Wiley** *23* (4a); *400E* (15); *562* (16) - **L.O. Williams** *42920* (4b); *399, 781, 3717* (7); *4339, 6097*, *7184, 12112, 41632* (8); *27506, 7136, 28449, 42666, 42756,* (9); *9468, 10722, 14517, 14661, 15100, 22295, 23032, 41246* (10); *8271, 15089* (11a); *24776* (11b); *6081, 10408* (13); *16851*, *26039* (14); *10343, 10736, 15956, 16928, 26436, 26703* (16); *8615, 8960* (17); *24919* (19); *10407, 16928* (20) - **R.S. Williams** *954*, *41822* (3); *773* (13) - **P. Wilson** *7309*, *8051, 11363* (4a); *169*, *9332*, *11309, 11467* (5); *350* (7); *11449* (15); *11421* (18) - **R. Wingfield** *13695* (10) - **J.R.I. Wood** *4134*, *4600*, *4839*, *10551* (3); *4088*, *4583, 11301* (9); *3756, 4392* (10); *3801, 4260* (13); *4734* (16) - **R. Woodbury** *s.n.* (4a); *s.n.* (18) - **R.E. Woodson Jr.** *1399, 1453* (13) - **A.L. Woolston** *G87, G.146* (9) - **G.J.N. Woronow** ***2460***, *4868, 5744* (9); *2460* (11b); *2706* (13); *2182* (16) - **R.D. Worthington** *17634* (7) - **F. Woytkowski** *8349* (7) - **C. Wright** *747, 748* (4a); C. Wright *3457* (5); *614* (9); *3465* (15); *749* (16); *51, 97, 3878* (18) - **R.P. Wunderlin** *322*, *8302,* 8445 (4a) - **J.J. Wurdack** *1048, 1096, 1807* (7); *1806* (9); *2674* (10) - **H. Wydler** *250* (7) - **K.N. Yoshida Arns** *971* (7) - **K. Young** *333* (9); *293* (10) - **S.M. Young** *23* (7); *75, 83* (9) - **T.G. 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Author's abbreviated biography

Riccardo Maria Baldini was born in Italy [Tuscany, Massa Marittima (prov. of Grosseto)] on March 15, 1958. After humanistic high school ("Liceo Classico") he began his academic studies at the University "La Sapienza" in Rome and later at the University of Florence where he obtained a degree in Natural Sciences with a thesis on the Rhamnaceae of Italy and Mediterranean area and later a PhD in Plant Biosystematics with a thesis on the genus *Phalaris* L. (Poaceae). After 12 years as curator at the Central Italian Herbarium (FI) he obtained the title of full-time researcher (Aggregate Professor), a position he has held to date, teaching Systematic Botany (Comparative Botany) for the course of study in Natural Sciences. After a period of research focused on the Mediterranean Flora and in particular on the Tuscan Archipelago, since 2002 he began studying Paleo- and Neotropical Poaceae and historical Neotropical collections. The meeting with the late teacher and friend Prof. Rodolfo Emilio Giuseppe Pichi Sermolli (1912-2005) brought him closer than ever to the field of Tropical Botany and the endless but interesting issues of botanical nomenclature. From 1992 to 2008 he acted as Assistant Editor of the Journal Webbia and from 2008 to present day as the Editor in Chief. He was also President of the FT herbarium (formerly the Italian Colonial Herbarium, also known as the Tropical Herbarium of Florence, currently the Tropical Herbarium Study Center). Between 2011 and 2018 he organized three International Symposiums on Tropical Botany with the aim of promoting interest in this field of study among the younger generation of botanists. His activity as a teacher-scholar continued abroad in Mesoamerica (El Salvador, Panama) and South America (Brazil). The taxonomic research activity has led him to frequent visits to numerous herbaria in Europe including BAS, BM, K, G, LINN, MA, MPU, P, PI, RO, UPS, W, and in non-European countries such as CAY, HUEFS, LAGU, MHES, MO, NY, PMA, R, VPT, US, in addition to collaborating with many others. The scientific production amounts to over 160 scientific papers as well as numerous participations in international conferences in Brazil, Chile, Denmark, El Salvador, Panama, Portugal, United Kingdom, United States. Recently he joined a team dedicated to the study of *Cocos nucifera* L. in the Pacific Ocean, in collaboration with the Montgomery Botanic Center (Miami, USA) and the Conservatoire et Jardin Botaniques de Geneva. After retirement, he expects to continue with his research interests in tropical Poaceae, the history of tropical botanical collections, and botanical nomenclature.

Figure 53. Riccardo M. Baldini during the expedition in Acre (2010, Brazil, Rio Chandless – Rio Purus).

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Edited by Riccardo M. Baldini (Editor in Chief)

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